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THE GEOGRAPHIC DISTRIBUTION OF CLOSELY RELATED SPECIES.[1]

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The botanical researches of the members of the New England Botanical Club are largely taxonomic and floristic. With some of us this is vocation, with others avocation. The majority perhaps pursue the study of plants in the field and make collections of them in herbaria for their own personal satisfaction. Floristic studies may properly be an end in themselves, whether followed as a business or only for recreation. In the latter case they need no further justification than the fine and pure pleasure they afford to those who love them for themselves. But the results of these studies, for whatever conscious motive pursued, may have an application and a destination far beyond our private aims. Collections of specimens and reports of distribution recorded in accessible journals by well-informed non-professional as well as professional botanists, may help materially in answering some of the largest questions of biological science. In this paper I hope to make it clear that refined taxonomy and most thorough-going plant geography may have a direct relation to the enormously difficult problem of evolution.

Organic geography has, indeed, already served the cause of evolution,— in aiding to secure general acceptation of the Descent Theory. Darwin and Wallace, drawing upon the works of taxonomers, were able to point to features in the distribution of

[1] A paper read before the New England Botanical Club at the meeting of Feb. 1, 1907. Published as Contribution from the Ames Botanical Laboratory, no. 6.

species which support the notion of common descent. Plants and animals, they said, occur upon the surface of the globe just as if they had originated by evolution, and in a manner unintelligible on the assumption of special creation. Species are universally found in the neighborhood of other species which they resemble; or to put this generalization in evolutionary phrase, species arise in geographic proximity to the species from which they may be supposed to have sprung. The geographic evidence was an important part of the testimony accumulated by Darwin ('59), to which he gives two of the fifteen chapters of the "Origin of Species." Wallace ('55) had already published an essay arguing for the evolutionary conception of organic history, the main thesis being this: "Every species has come into existence coincident both in time and space with a pre-existing closely allied species." Thus the evolutionist has been under deep obligation to the taxonomer from the beginning.

The obligation is likely to be much increased with the lapse of time. I do not agree with D. H. Scott, that the determination of the actual course of descent is the ultimate, or chief, object of the scientific systematist.[1] The fact of evolution being admitted, and the course of evolution having been ascertained, there still remains the question, "By what methods have new forms emerged from old ones?" — a subject not less interesting or important than the others, from any point of view. It seems to me, furthermore, that the final goal of phytogeography is not reached in the reconstruction of the continents and islands of former epochs, and the reviving of ancient states and changes of climate, through the study of the history of the vegetation of the earth; nor is its purpose satisfied in teaching us through its ecological aspects, that plants are marvellously and multifariously adapted to their environments. Biologically considered, there is a still more valuable product yet to be yielded by these sciences. Organic geography will, I believe, unite with systematic botany and zoölogy and with experimental morphology in composing the solid basis of an adequate theory of evolution.

[1] The present Position of Palæozoic Botany, Lotsy's Progressus Rei Botanicæ, **1**: 139 (1907).

The finely discriminative work of modern taxonomers, much as it confuses and discourages students of other aspects of biologic science, is necessary for several reasons but especially is it necessary from the point of view of the evolution problem. Doubtless systematic and experimental work will be more frequently coöperative henceforth, and such studies as those of Alexis Jordan, de Bary, Rosen and Wittrock will be repeated with many of the so-called polymorphic plant groups by students of the greater problem.

This view is apparently opposed to that lately expressed by a prominent worker in experimental evolution, who seems to deny this applicability. "The underlying fault," he says, "consists in the fact that taxonomic and geographic methods are not in themselves, or conjointly, adequate for the analysis, or solution, of genetic problems. The inventor did not reach the solution of the problem of the construction of a typesetting machine by studying the structure of the printed page, but by actual experimentation with mechanisms, using printed pages only as a record of his success. Likewise no amount of consideration of fossils, herbarium specimens, dried skins, skulls, or fish in alcohol may give any actual proof as to the mechanism and action of heredity in transmitting qualities and characters from generation to generation, although from such historical data the general trend or direction of succession may be traced." — MacDougal (:06, p. 4).

Nevertheless, it may be shown that, while such studies are not in themselves adequate to the solution of genetic problems they have a very high corrective and evaluatory worth.

Geographic studies founded on an exact taxonomy have a corrective function. It is axiomatic that no theory having its origin in experiment can be accepted if it seems to be in fundamental discord with what we know of the present disposition of the organic world. For example, the theory of Mutation as developed by de Vries cannot be accepted for the animal kingdom, if, as seems to certain zoölogists, it is irreconcilable with the facts of the distribution of animals. And even if an hypothesis is not positively excluded by the facts, it may be weakened or practically nullified by comparison with large bodies of facts

gathered broadly; so that we may fairly ask the experimental school to admit that results, however well proved for the conditions established by the experimenter, ought to be assigned little worth if they find only a trivial correspondence in nature at large. We make the same demand of the physiologist with respect to such a phenomenon as geotropism, for instance. The extended study of this form of irritability has its justification only in the fact that plants in nature so widely show the effects of geotropism in their forms; the value of the experimental results is great because the phenomenon is manifestly widespread in free nature, being observable in the erect attitude of countless main axes in field and forest, in the fixed angles of side stems, the vertical descent of tap-roots, etc., etc. In like manner a true theory of specific origins should find strong confirmation in the study of the broadest aspects of plant and animal life. Every grand agent of specific modification should leave its distinctive mark upon the character of life as a whole, and if we rightly apprehend the nature of the agent we may expect to be able to distinguish its special mark or effect when we know plants and animals thoroughly. I think that it will appear from considerations which I now bring before you that the distribution of species must have peculiarities corresponding to the particular class of evolutionary forces which have been at work. If this be so, suitable studies in geographic taxonomy must possess high evaluatory worth when we wish to estimate theories of evolution.

THE EFFECTS OF DIFFERENT EVOLUTIONARY AGENCIES UPON SPECIFIC DISTRIBUTION

Let us examine the necessary effects of the chief supposed evolutionary agencies upon the character of specific distribution; and first contrast Natural Selection in Darwin's stricter sense with Mutation, in this regard. Natural Selection works within specific limits. Its materials are the small, or individual, variations within the species. By the accumulation of these variations as they occur from generation to generation new characters are built up. The change in a species is slow and the whole species within a given competitive area moves along together. When

we consider that sufficient change has occurred to warrant the epithet 'new,' as applied to the condition of the group, we find that the new species has risen upon stepping stones of its dead self, since the survival of the fittest has had its converse in the extinction of the unfit — that is, the 'old' species —; and in the given area only a single new species is found replacing the vanished old one. For any given area of competition the transforming effect of Natural Selection then, is monotypic. Romanes (:06, ch. I.) clearly states the truth that Natural Selection without isolation effects monotypic evolution, and only by the aid of isolating factors of some kind results in polytypic evolution. Nägeli's earlier exposition of the monotypic effect of Natural Selection was explicit (Nägeli, '73).

On the other hand Mutation breaks the species and momentarily at least, must give a polytypic aspect to the group within a specific area. The parent species is contemporaneous with the new species to which it gives rise. The new and the old stand side by side for a time, without geographic isolation and in general without isolation of any sort. This is the primary condition. Subsequently competition may leave only one of the several original forms in an area. In some instances topographic (ecological) separation of the mutants, or chronal isolation in respect to flowering or breeding time, a physiological isolation may be the immediate result of Mutation. But as a rule the first effect of Mutation must certainly be the allocation of closely related species, or kinds, in the same area without any sorting or separation.

If we compare Orthogenesis, acting under guidance of the environment, with Natural Selection on the one hand and Mutation on the other, we see that Orthogenesis must in many respects agree with Natural Selection rather than with Mutation as concerns the distribution of its products — species. Throughout a single region of uniform ecological character the effect of environmental moulding, so-called, upon a given organic stock must be monotypic. But if the ecological conditions are diverse in a geographic district, as they always are when the surface is varied, we may expect to find as many kinds of plants or animals derived from a single stock as there are ecologically different environ-

ments in the district; or, if interbreeding suffices to reduce the diversity in some degree, at least several kinds perferring different habitats. While in the broader geographic sense this effect would be polytypic, in that any geographic district might have several different closely allied types, each type would fit a particular set of conditions; there would be definite allotment and topographical separation of the derivative species, and each ecological field would present a monotypic aspect. A distribution quite distinct from that due to recent Mutation would be found.

Thus while the geography of species may or may not be decisive as between the evolutionary theories known by the names Natural Selection and Orthogenesis, both these modes are distinguished from Mutation in the immediate effects which they have upon distribution. Such specific distribution as Moritz Wagner asserted to be universal or almost universal, if it could be proved, would be practically fatal to the Mutation Theory regarded as a general explanation of specific evolution.[1]

It is hard to see on what ground the experimentalists can deny the competence of geographic evidence. Indeed they appear at times to recognize the propriety of the appeal to nature; De Vries refers to Draba, Viola and similar groups, and MacDougal in the paper already cited alludes to studies of plant distribution and adduces the case of closely related Opuntias in the Arizona desert. The distinguished zoölogist who recently assumed to pass upon the merits of the Mutation Theory, evidently without

[1] Yet Darwin (Orig. Sp., ch. IV.) in his theory of Divergence of Character, seems to allow polytypic evolution within an area by means of Natural Selection. He thinks geographic isolation unnecessary. Weismann (:04, 2: 338) argues against the necessity of isolation and for a polytypic condition as possibly arising by Natural Selection, alleging in support of this view sexual dimorphism, and polymorphism in species of animals. To which it may be replied that we do not know whether the diverse forms in the same species of animals have arisen by Natural Selection. In the absence of evidence, the contention becomes a theoretical one, in which Romanes ('86, pp. 343, 386), Gulick ('88, pp. 202–206) and Nägeli seem to have the clearer views, and I have accepted their opinion. Whichever side is taken, *it has to be allowed that a uniformly monotypic geographic distribution excludes Mutation.*

much knowledge of De Vries's work and apparently after a reading of only the popular lectures published in this country,[1] was at least thus far right, that he searched for indications of mutation in the distribution of animals. The evidences should be found even in museums, providing the museums are representative, and providing mutation is a sufficient explanation of the origin of species.

The Necessity of Isolation: Mendelian Inheritance

Before coming to an examination of the facts as they are represented by writers, it will be well to consider for a moment a theoretical side of the subject, namely the supposed *necessity of isolation* as a factor in the evolutionary process. Granting that new forms may appear upon the scene by Mutation, what is to become of them? How can Mutation be said to originate new species — that is, stable groups — if through interbreeding the mutants are at once swallowed up by the parent species with which they grow commingled? The opponents of the Mutation Theory hold that the isolation which the experimenter practices in his garden by means of paper bags, etc., is lacking in nature and that this difference between the garden and free nature vitiates the experiments.

The need of isolation is well, and for the present sufficiently, discussed in the writings of Romanes and Gulick; the latter has treated every form of isolation in an exhaustive fashion, chiefly from the theoretical standpoint and upon the basis of the very limited knowledge of heredity of a few years ago. The conclusion of these authors is that some kind of segregation or isolation is necessary for the success of a new race. While Wagner ('89) saw only spatial isolation as giving the needful security, Romanes (:06) and Gulick (:05) have shown, as well as can be shown deductively, that other forms of isolation may suffice, such as

[1] Is it too much to ask that those who undertake to discuss deVries's theories shall read his evidence? The lectures in English (Species and Varieties, Chicago, 1905), doubtless serve a useful purpose in popularizing, but incidentally have done some harm in leading certain critics to suppose that they may find therein an adequate exposition of principles and evidence.

difference of breeding time, difference of local habitat, and physiological properties precluding inter-breeding. The clear discussions of Romanes and Gulick have rendered superfluous much in recent disputes on Isolation and Evolution.

Lately new conceptions in the theory of heredity have materially changed the conditions of the argument. Experiment has shown that new characters may not be immediately swamped by promiscuous breeding, but may on the contrary, in the fusion of new and old races, predominate in full force over old characters which they sometimes have the power of entirely subduing.[1] While this result is very suggestive, too little is as yet positively known to make an extended discussion at all profitable. Those who are inclined to argue the matter may well take caution from Davenport's opinion on the integrity of unit characters. "While admitting, thus, the reality of unit characters, the further study of the evidence of hybridization in poultry has led me away from the conception that they are rigid and immutable as atoms are, which may be combined and recombined in various ways and always come out of the process in their pristine purity. This is by no means the case. Very frequently, if not always, the character that has been once crossed has been affected by its opposite with which it was mated and whose place it has taken in the hybrid. It may be extracted therefrom to use in a new combination, but it will be found to be altered. This we have seen to be true for almost every characteristic sufficiently studied — for the comb form, the nostril form, cerebral hernia, crest, muff, tail length, vulture hock, foot feathering, foot color, ear lobe, and both general and special plumage color. Everywhere unit characters are changed by hybridizing.

"How does this fact bear on the rival theories of evolution? It has an important bearing on them. It is not in accord with the statements of de Vries quoted above: 'The characteristics of organisms are built up of units that are sharply separable one from another,' and 'Transitions exist between the units as little as between the molecules.' Single comb is one unit and pea

[1] Besides the Mendelian results see also de Vries (: 03, **2**, p. 396 *et seq.*) on the crossing of mutants with the parent species.

comb is a different unit, but they are not sharply separable. Crest and no crest are units, but they run into each other in hybridizing. Unit characters may show transitions, and, if so, they may have originated gradually, so far as I see. It does not follow that they must have originated gradually" — Davenport (:06, p. 80).

Castle and Forbes's results with guinea pigs indicate the same modifiability of unit characters. These authors (:06, p. 13) say: "From the foregoing observations it is clear that, while the long-haired and short-haired conditions are sharply alternative to each other in heredity, the gametes formed by cross-breds are not in all cases pure. Frequently they consist of a blend or a mixture of the two alternative conditions, constituting in effect a new condition intermediate between the other two. A study of other characters alternative in heredity yields results somewhat similar.

"Albinism is, in heredity, the most sharply alternative of characters, yet cross-breëding between albino and pigmented guinea-pigs may modify the character both of the albino race and of the pigmented one. This modification may take on a variety of forms, as has elsewhere been pointed out (Castle, :05). It may result in the production of mosaics (pigmented animals spotted with white), or of albinos with a modified peripheral pigmentation, or of albinos visibly like their ancestors but transmitting a different set of latent characters. Again, the rough or rosetted coat of certain races of guinea-pigs is sharply alternative to smooth coat, yet cross-breeding of rough with smooth races may induce curious modifications of the rough character or produce smooth individuals bearing the merest trace of the rough character.

"All these facts are in harmony with the hypothesis, for which there is strong evidence on the cytological side, that each separately heritable character is represented by a different structural element in the germ (egg or spermatozoon). In fertilization the paternal and maternal representatives of a character become more or less closely united, this union persisting through all subsequent cell-generations until the new individual forms its sexual elements. At that time the paternal and maternal representatives of a character separate from each other and pass into different cells.

"But the paternal and maternal representatives of a character may in the meantime have exercised on each other a considerable influence. In the case of some characters, as ear-length in rabbits (Castle, :05a), they completely blend and intermingle, so that a new character is produced strictly intermediate between the conditions found in the respective parents.

"In other cases the modification may be slight, as if the paternal and maternal representatives of a character had been scarcely more than approximated. Sometimes in cases of alternative inheritance no influence of the cross is observable in certain of the 'extracted' individuals, but if any considerable number of individuals is examined, others will be found in which the cross-breeding manifests its influence. From this we conclude that gametic purity is not absolute, even in sharply alternative inheritance."

These are very interesting qualifications of the Mendelian principle of gametic purity. They suggest that new characters might be swamped by repeated crossing, unless they were of such overwhelming importance that they quickly won out in the struggle for existence, to the immediate extinction of the bearers of the older alternative characters. However, discussion may here well wait upon further discovery.

But this may be said: If characters are gradually modifiable, time becomes a necessary element in experiments on evolution and possibly long periods of time may be needed for the demonstration of certain slow natural processes. For the present we may well hesitate to accept the conclusion that Mutation is the sole and only possible mode of evolution. Refreshing as the new method of research is, in the midst of oceans of tiresome speculations, and most valuable and even absolutely indispensable as the results already are, the latter are certainly small compared to the bulk of our ignorance regarding morphogenetic processes. Those who are free from inexpugnable prejudice on the one hand and from infatuation with new ideas on the other, will look for some independent means of estimating the probable significance of the new theories. It is the chief object of this paper to suggest that such estimation may be rested upon the evidence of organic geography when the evidence is available in sufficient body.

If we were right in what was said above about the specific effects of different modes of evolution upon distribution, the first question to be asked of the geographer is this: Are species universally so distributed that each one occupies a region of its own, or a habitat of its own; so that even the nearest related species are strictly separated in space, either in the broad geographic sense, or at least topographically?

It is to be noted that the inquiry has two steps, or stages. The first relates to the distribution of organisms in the broader sense, and it is inquired whether closely related species are found in identical districts, or have largely coincident ranges, in many cases. The adherents of the Mutation Theory expect to find a considerable proportion of such instances. Certain of its opponents have believed that the advance of the theory might be blocked on this first level. But if their efforts fail here they are prepared to fall back upon the second line of defence. The second stage of the inquiry relates to topographical distribution, or distribution in relation to ecological conditions, and asks whether any of the allocated forms — if some are found — exist side by side without even local segregation. Disciples of de Vries expect that instances will occur in such numbers as to satisfy the demands of their theory; while the opposite party thinks that practically no instances will be discovered giving countenance to the idea of Mutation. They expect that all cases of general geographic coincidence of range will be accounted for by ecological segregation, affording practical isolation; and so hope to withstand the final assault of the Mutationists.

The application of the botanical evidence presented in this paper is to the first stage of the inquiry. Some of it is manifestly applicable to the second stage also.

Specific Distribution in the Animal Kingdom

We may briefly review some of the chief contributions to our knowledge of the distribution of animal species. Moritz Wagner, Professor of Zoölogy in Munich, perceived the close relation which distribution may have to the problem of evolution and began to publish upon this subject very shortly after the appear-

ance of Darwin's Origin of Species, first as an advocate of the theory of Natural Selection, but shortly as its opponent. Through twenty years of controversy he insisted upon the inadequacy of Natural Selection, and as the prime factor in the diversification of species sought to substitute Spatial Separation and to establish his own Law of Migration and Colony-formation. He supposed a new species to arise by the migration or escape of a single individual or of a pair from the domain of the old species into new territory, where in geographic isolation and freedom from the influence of the old stock a new race might be founded. The divergence of the race from the old type he supposed to result (Wagner, '89, pp. 286–295, 401) (1) from the individual peculiarities of the parental pair or individual, which peculiarities in the absence of the normalizing influence of interbreeding with the whole body of the old stock would necessarily become accentuated; and, (2) from the new environment. His theoretical views, which throughout are questionable, are of less consequence than the facts which he adduced in their support; the facts indeed upon which he first formed these views. Wagner himself was a traveler, observer, and collector in several parts of the world and continually recurs in his writing to his experience in the field with regard to endemic, narrowly restricted species-forms and contant local varieties occurring in overwhelming numbers. His illustrations are drawn from all classes of animals and to some extent also from plants. He represents specific distribution as having a strictly mosaic or chain-like character. Everywhere we find vicarious species and local races in separate habitats. The facts are presented at great length and with careful detail, and seem to form a consistent body of knowledge, which impresses one as being pregnant with a rational principle of wide import.

Mr. C. H. Merriam about a year ago addressed the zoölogical section of the American Association for the Advancement of Science on the topic, "Is Mutation a factor in the evolution of the higher vertebrates?"— (Merriam, :06). While many of the arguments and conclusions regarding evolutionary processes belong, to my mind, too largely in the conjectural category, and while this author's grasp upon the real character of de Vries's work and upon his theory seems comparatively feeble, the data

of distribution brought forward for several groups of mammals are valuable. Dr. Merriam considers the geographic relations of certain American rats, chipmunks, and ground squirrels; and refers besides to other groups. His representation of specific distribution agrees with that held by Wagner, with a qualification. Merriam shows that the mammals in question occupy distinct areas with very little exception, but that the areas often overlap, and that the overlaps are likely to constitute narrow transition zones characterized by the presence of intergrades. Actual physical barriers are often wanting.

President David Starr Jordan has also discussed the Mutation question from the standpoint of organic geography and assembled from his own experience and that of others a considerable body of evidence regarding birds, while he himself speaks for fishes (Jordan, :05). His paper, which appeared in Science a little more than a year ago, contains some extraordinarily sweeping assertions. He says: ". . . . Moritz Wagner (1868) first made it clear that geographical isolation (räumliche Sonderung) was a factor or condition in the formation of every species, race, or tribe of animal or plant we know on the face of the earth." The principles set forth by Wagner "have never been confuted,[1] scarcely even attacked, so far as the present writer remembers, but in the literature of the present day they have been almost universally ignored." The question is much discussed whether minute variations may serve to establish a new species in the presence of a parent species, or whether wide fluctuation or mutation may do so. "In theory either of these conditions might exist. In fact both of them are virtually unknown. In nature a closely related distinct species is not often found quite side by side with the old. It is simply next to it, geographically or geologically speaking, and the degree of distinction almost always bears a relation to the importance or the permanence of the barrier separating the supposed new stock from the parent stock." "The contention is not that species are occasionally associated with

[1] See the works of Darwin ('72), Romanes, Weismann ('72), and Nägeli cited in the Bibliography. Weismann's paper relying upon the case of *Planorbis multiformis* in the Steinheim chalk should be considered in connection with Hyatt's Memoir on the same form ('80).

physical barriers, which determine their range, and which have been factors in their formation. It may be claimed that such conditions are virtually universal. In a few cases, a species ranges widely over the earth, showing little change in varying conditions and little susceptibility to the results of isolation. In other cases, there is some possibility that saltations, or suddenly appearing characters, may give rise to a new species within the territory already occupied by the parent form. But these cases are so rare that in ornithology, mammalogy, herpetology, conchology and entomology, they are treated as negligible quantities. In the distribution of fishes the same rules hold good, but as the material for study is relatively far less extensive and less perfectly preserved than with birds and insects, we have correspondingly less certainty as to the actual traits of species and subspecies, and the actual relation of these to the intervening barriers."

President Jordan summarizes the distribution of species in a law, as follows: "Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort." That the intent of the law involves both animal and vegetable kingdoms seems clear from the context.

President Jordan says that his conclusions, much as they differ from *a priori* judgments or the results of experiment, are the unavoidable outcome of the study of distribution, and that they are as a matter of fact "accepted as self-evident by every competent student of species or of the geographical distribution of species."[1]

Taking the facts of animal geography as they appear in these several essays, typical of a larger number which might be cited, we may say that as a whole they militate against the operation of Mutation in any wide sense in the animal kingdom. This conclusion is not prompted by the attitude of certain of the zoölogists mentioned, who seem to have made but a cursory study of

[1]In a later note in *Science* (N. S., **22**, p. 873) Pres. Jordan modifies his position somewhat, as regards the exclusive agency of spatial isolation and the need of actual physical barriers; but his representation of specific distribution in the animal kingdom is not recast.

the Mutation Theory, but is drawn from the geographic evidence. It is, however, true that the evidence is rather scanty. Moreover there are some exceptions to the general law of distribution, and if these exceptions should, upon further research become very numerous, the prejudicial force of the law would be much diminished. But from the evidence at hand we may infer the very general truth that animal species are distributed according to Jordan's law of geographic isolation; that when exceptions occur, the exceptional species are taken over into some other category of isolation. The nearly universal patch-work character of specific chorology — as at present depicted in the works of zoölogists — strongly suggests the gradual spreading out of individuals over the surface of the earth, their settlement here and there in isolated districts or topographically distinct stations, where shielded from promiscuous intercrossing they have undergone transformations, which have been different in the different areas; transformations which, advancing by whatever forces or conditions, whether those of Natural Selection or of orthogenesis, or what-not, have advanced with even front. This suppositious history is that which forms itself in the imagination of most students of animal geography and has appealed most strongly to me as I have reviewed the literature of the subject.

The Distribution of Plants.

Turning now to the vegetable kingdom we find, first, that there have been few or no exhaustive essays dealing with the question of specific distribution in relation to the theory of evolution. In the second place, it may be said at once that when botanists have turned their attention in this direction their views generally do not coincide with those of the zoologists as to the nature of the facts.

Nägeli ('73) opposed Wagner in a paper of which the purport is succinctly expressed in the title, "Die gesellschaftliche Entstehung neuer Spezies," — the social origin of new species. This eminent botanist stoutly opposed Wagner as to the general character of specific distribution, to the study of which he gave much time in the field for several years. He calls particular attention

to the association of species of plants and their varieties upon the same ground, and states that when one form replaces another in consequence of change of ecological conditions within the same district, the replacing form is not related to the other in the closest grade of affinity, but in some degree more remote. He clearly recognizes the intimate relation of distributional studies to the question of evolution.

There is a little bit of evidence from Wallace (:00, p. 391). He says he made inquiries of two experienced English botanists to find whether well-defined varieties occupy areas to the exclusion of the type and do not occupy the area or only a very small one with the type. Only one such case was found in England. Wallace's conclusion is that such varieties of plants occupying considerable areas to the exclusion of the type are not common.

Asa Gray ('59, p. 193) expressed the following opinion: "Whether capable of scientific explanation or not it is certain that related species of phænogamous plants are commonly associated in the same region or are found in comparatively approximate areas, however large, of similar climate."

The case of *Draba verna* L., is most interesting. As is well known, about two hundred distinct species, or at least kinds, of Draba have been distinguished within the limits of the original Linnæan species *Draba verna*. These numerous forms were studied in cultivation by A. Jordan, and later by De Bary and F. Rosen. They are found to come true to seed, and for this reason are by these authorities spoken of as species. Their geographic distribution is discussed by both Jordan ('73) and Rosen ('89, p. 613). The conclusion is that as a rule the forms which resemble each other most are found in the same stations. The joint occurrence of next related species is indeed a fact which particularly impressed both of these writers. Rosen thinks that it is very unlikely that these closely related species originated separately and by chance came to be associated in the fashion in which they are now found. Such an explanation might serve, he says, if one or two cases only were to be explained; but it becomes absurd when we consider that the concomitance of next related forms is wide-spread. Rosen ends his account of this group of Draba species with a very clear statement of the mutative origin

which he is obliged to assign to these forms; without, of course, using the terms of the Mutation Theory, which he partially anticipates by several years. "The Erophila [Draba] species owe their existence to the free variation of their forefathers. This consists not in a mere heightening or further development of single characters, but variation fashions new characters and combines old characters in new ways. Therefore the forms which arise from species do not intergrade."

He says that, while Selection plays no part in the origin of these forms it operates upon them after they appear. And of the laws which must control this sort of variation he speaks as follows: "Variation is not blind, vaguely working in all directions, but is obviously determined by laws unknown to us: for we are obliged to assume that the same or similar combinations of next-related forms have arisen in different places. But what can these laws be?" It is most interesting and significant that *Rosen is led to these de Vriesian conclusions through floristic and geographic studies.*

The following excerpt from A. Jordan ('73, p. 4) has so direct a bearing upon our argument that I give it entire: "Ayant observé dans leurs stations diverses, pendant plus de trente années, une foule de végétaux de toutes les familles et de toutes les catégories, des plantes annuelles ou vivaces, bulbeuses ou aquatiques, des arbres ou des arbustes, j'ai pu constater presque partout que lorsqu'un type linnéen, vraiment indigène dans une contrée, y était commun à ce point qu'on pouvait le citer parmi les plantes caractéristiques de la végétation d'une certaine étendue du territoire, ce type y était presque toujours representé par des formes diverses, plus ou moins nombreuses, *croissant en société et pêle-mêle* [ital. mine]. L'observateur superficiel, qui parcourt le terrain, n'est frappé que des ressemblances de ces diverses formes; il n'aperçoit pas leurs différences, ou, n'y attachant aucune importance, il ne s'arrête pas à les considérer attentivement; il croit n'avoir affaire qu'à un type unique, susceptible de quelques modifications accidentelles et sans valeur. Tandis que celui qui observe avec attention peut aisément se convaincre, sur les lieux, que ces modifications apparentes se retrouvent sur des individus divers, tous parfaitement semblables entre eux. Si,

pour pouvoir continuer et compléter son observation, il arrache des pieds vivants de chacune des formes qu'il a pu distinguer et les replante ensuite, dans un même lieu, afin de les suivre dans tous leurs développements, il se convaincra bientôt qu'elles présentent des différences appréciables, dans tous leurs organes S'il sème leurs graines, il les verra se reproduire avec une parfaite identité de caractères.

"Voilà le fait que j'ai pu constater moi-même mille fois, que j'ai fait constater dans les lieux que je ne pouvais visiter, en France, en Corse et en Algérie ou ailleurs, par divers botanists qui m'ont envoyé soit des graines, soit des pieds vivants de formes nombreuses, recueillis dans les mêmes station et appartenant aux memes types linnéens. Je ne dis pas que les plants communes soient toutes également et partout diversifiées. Il y a, sous ce rapport, de grandes differences entre elles. Je dis seulement que *le cas où elles présentent diverses formes croissant en société est le cas le plus ordinaire* [ital. mine], et je crois que ce fait paraîtra clair, patent, indiscutable, à quiconque prendra la peine de le vérifier sérieusement."

In the literature of this subject, as far as I have read it, essentially the only writers who insist on the isolation of nearly related kinds of plants are the zoologists. Their assertions are not, however, supported by evidence from the vegetable realm.

I have examined the distribution of North American Orchidaceæ from the standpoint of this paper. Furthermore, I have consulted with several specialists in different groups as occasion offered. Several members of this club have given me information with permission to publish it along with the evidence gathered by myself. I may take the groups in sequence.

For Algæ, Mr. F. S. Collins speaks as follows in regard to their general distribution and in particular the distribution of nearest related species: "As regards fresh water algæ, it almost seems as if geographical limitations did not exist. Of course this is not entirely true, but the area of distribution in the case of the great majority of fresh water algæ is vastly greater than in the

case of most flowering plants.[1] The limitations seem to be those of temperature, exposure, character of attachment, and to a less degree, geological characters. Take the genus Vaucheria, for instance. The last serious work is by Götz; a study of the species of Vaucheria in the neighborhood of Basel, Switzerland. There are 12 species there; 8 of them occur in England, 6 in the New England States, 7 in California. Only three other fresh water species are recorded for North America; one is a European species, found in the West Indies but not elsewhere so far on this continent; the other two are from California. Now these two species, growing together, belong to the same subgenus, and I know of no described species that I should say belonged in between them. Take the genus Spirogyra. The best book on this is that of Petit, Spirogyres des Environs de Paris. He includes 37 species; of these 34 have been found in North America. We have also five other species; three of them are European, though not found about Paris; the two others are from Greenland and Florida respectively. It is much the same with all the fresh water algæ; of the very inconspicuous species, the records from distant stations are not so abundant, but that is largely because these minute forms have been little studied outside of Europe.

"As to the marine algæ, the difference geographically is much greater. It would seem strange that marine algæ on the two sides of the Atlantic, should differ much more than the fresh water algæ of the two continents, but such is the fact. Still the resemblances are much greater than with flowering plants. And there are many instances where closely allied species or varieties have practically the same range. I will give a few such pairs, and in each case there seems to be no species or variety anywhere else that would stand between the two in question.

"*Cladostephus verticillatus* and *C. spongiosus* have the same range, in temperate waters on both sides of the Atlantic. They are the only species of the genus in that range. *Fucus edentatus* and *F. evanescens* have their headquarters in high arctic regions,

[1] Compare Alph. De Candolle, Geographie Botanique, **1**, p. 499: "Nous arrivons ainsi à une loi importante, savoir que *l'aire moyenne des espèces est d'autant plus petite que la classe dont elles font par.ie a une organisation plus complète, plus développée, ou, selon l'expression usitée, plus parfaite.*"

extending to Great Britain, New Jersey and California. *Myriotrichia filiformis* and *M. clavæformis* have practically the same range as the Cladostephus species. *Ralfsia borneti* and *R. verrucosa* have a slightly more northern range on both sides of the Atlantic. *Phyllophora brodiæi* and *P. membranifolia* range from France and New Jersey to Norway and Labrador. *Polysiphonia violacea* and *P. fibrillosa* from Virginia to Maine, from the Mediterranean to Scotland. *P. harveyi* and *P. olneyi* are American species, or possibly varieties of the same species; they have the same range as *P. violacea* and *P. fibrillosa*; wherever I found one, I should expect to find the other.

"I could keep on for some time in this way, but will give only one more instance; that is a group of species in the genus Antithamnion, one of the most beautiful of the red algæ. On the European coast *A. plumula* ranges from Morocco to Great Britain; *A. cruciata* about the same; *A. floccosa* from the English channel to high arctic regions; *A. boreale* from the Faroes north; *A. pylaisæi* from Norway north. On the American coast *A. plumula* and *A. cruciatum* range from New Jersey to Cape Cod; *A. floccosum* and *A. boreale* from Cape Cod to Greenland; *A. pylaisæi* from Long Island Sound to Greenland; *A. americanum* from New Jersey to Portland, Maine. On our Pacific coast *A. floccosum* ranges from California to Alaska; *A. boreale* from southern Alaska to high arctic regions; *A. pylaisæi* from Washington north. Now these are all so closely allied that Rosenvinge some time ago proposed to unite them all under the older name, *A. plumula*. He is a man with a strong tendency toward uniting, it is true, and has since concluded that *A. cruciatum*, and possibly *A. floccosum* are distinct; but at any rate, this shows how closely allied they are.

"Some things about algæ seem very much like supporting the mutation theory; when the same species occurs in widely distant stations, we sometimes find with the type exactly the same varieties and forms."

Dr. Evans, while lacking the opportunity to pay very extended attention to the subject, has given me the following indication of the distributional conditions in Hepaticæ. "One of the best examples of a cognate pair of species is *Leptolejeunea elliptica*

and *L. exocellata*. The first of these species is very widely distributed in tropical America, growing on the upper surface of thick and glossy leaves. The second species is less abundant but nearly always occurs mixed with the first.

"Among northern species *Lophozia barbata* and *L. lyoni* are closely related and often grow together, although each retains its distinctive characteristics. The same is true of *Gymnomitrium concinnatum* and the much rarer *G. corolloides*; of *Sphenolobus exsectus* and *S. exsectæformis;* of *Anthoceros levis* and *A. punctatus*.

"As a group of related species I might mention the ventricosa-group of the genus Lophozia. This contains about half a dozen closely related species, most of which are circumpolar in their distribution. *L. ventricosa*, *L. alpestris*, *L. porphyroleuca*, *L. longidens* and *L. confertifolia* are all known from New England, being most abundant in mountainous regions. Of these *L. porphyroleuca* and *L. longidens* grow on rotten logs, and the others on moist rocks, although *L. longidens* is equally at home on either substratum. Although I have no definite data that these species actually grow mixed in North America, their ranges coincide to a greater or less extent with some overlapping.

"Unfortunately our information is not very full at present about the distribution of many species. Only a few regions have been at all accurately studied, and I feel sure that further study would considerably lengthen the short list I have given."

Mr. A. A. Eaton has given me several examples from Equisetum and Isoetes. "*Equisetum fluviatile* is circumboreal in its distribution. No third form stands between this and *E. palustre*, yet the latter has practically the same range. *E. scirpoides* and *E. variegatum* are a cognate pair, and yet both have in general the same range throughout the northern part of both hemispheres. *E. variegatum* has a variety, *E. variegatum jessupi*, distinguished by anatomical characters. Its range, Vermont to Minnesota, is quite covered by that of the species. *E. lævigatum* has a near relation, without an intermediate, in *E. hiemale intermedium*, and this on the other side is next to the variety *affine*. The last of the trio is wide-spread in northern North America and overlies the other varieties, which also essentially coincide in their ranges. *E. arvense* is found in Europe, Asia, N. America to Virginia and

southern California. Its near of kin (without intermediate), *E. telmateia*, is found with it (broadly speaking) in Europe and California. Starting with *E. pratense* a next-related species is *E. sylvaticum*. The former belongs to northern Europe, Siberia, Alaska, Canada, the Rocky Mountains, Labrador, and southward to Massachusetts and New Jersey. The other is circumboreal, covers the range of the first and with us goes somewhat further south to Virginia.

"In Isoetes we find the following coincident ranges of close relatives. *Isoetes tuckermanni* is found quite plentifully in New England and completely overlies the range of its varieties *harveyi* and *borealis*. *I. Engelmanni* is found plentifully throughout the region east of the Appalachian range, from New Hampshire and Vermont to Pennsylvania, extending sparingly to Georgia. It overlies the ranges of its varieties *caroliniana, fontana* and *valida*. *I. canadensis* is found from Pennsylvania to Maine and Quebec, appearing again in British Columbia. Its next of kin in the genus is *I. engelmanni*, whose range for the most part it covers, and the two species are not rarely found commingled in the same pond. *I. bolanderi* is found from Wyoming to California and Washington. Its next of kin would appear to be *I. pygmæa* of the Mono Lake region of California, and the two species were found by members of the King Expedition in contiguous areas. It may be supposed that *I. pygmæa* is an abnormal form of *I. bolanderi* and hence not competent in this relation, but the next of kin of *bolanderi* is *I. echinospora* var. *braunii*, which overlies the range of *bolanderi*, but is widely distributed otherwise in North America."

I have inquired of President Brainerd about the conditions in Viola, and particularly whether pairs of closely related species are found within the same ranges. He answers: "Many pairs of species in Viola closely allied and nearly co-extensive in range are to be found." He mentions six of them; viz. (1) *V. fimbriatula* and *sagitata*, (2) *V. palmata* and *papilionacea*, (3) *V. septemloba* and *emarginata*, (4) *V. lanceolata* and *primulæfolia*, (5) *V. ranifolia* and *incognita*, (6) *V. arenaria* and *conspersa*. These are without intermediate species says President Brainerd, but they have intermediates resulting from hybridization, found in the same localities with the species.

To Professor Charles Sprague Sargent I am indebted for interesting information as to the distribution of North American Cratægus. As is well known, numerous species have been distinguished within the last few years, of which some five hundred have been named. These species are readily and unmistakably recognized by special students of the genus, by means of floral characters such as number of stamens, color of anthers, form of inflorescence, etc.; by fruit characters, configuration of nutlet, time of blooming and fruiting, character of foliage, veining, presence or absence of hairs, etc.; traits which appear to be constant and reliable as shown by extended observation in the field and by cultures of seedlings carried on now for a number of years at the Arnold Arboretum. In these cultures, the sowings from the several species result in crops of seedlings of remarkable uniformity within the limits of each species, and in the instances in which the seedlings have flowered and fruited, of notable conformity to parental type. This result must certainly diminish the scepticism with which the proposal of such a vast number of species within the one genus has rather naturally been met in some quarters.

In answer to the question whether the nearest related species are separated, as the law of D. S. Jordan and of Wagner would require, Professor Sargent replies in the negative.

In the genus as it is represented in North America several groups are distinguished, which in part correspond to the species of the older writers, and which may be readily recognized by anyone with a little attention· such are Crus-galli, Punctatæ, Æstivales, Tenuifoliæ, Pruinosæ, Intricatæ, Flabellatæ, Anomalæ, Molles, Tomentosæ, etc. These groups are in general fairly well restricted to particular geographic sections. For example, the Tenuifoliæ, the largest group in the northeast, do not extend west of the Mississippi river, or go southward except along the mountains. The Flavæ are found only in the southeast. The Intricatæ are most numerous in eastern Pennsylvania, extending along the mountains southward to the end of the Alleghanies, northward into Vermont, and westward through New York and Ontario to southern Michigan, within which distributional area they mingle with all the other northern groups. In some cases a group

predominates in a region, in other regions several groups are nearly equally represented. Within each group, divisions can be made; but in the case of these divisions geographic separation does not obtain, since species of all the divisions of a group are likely to occur in any part of the general territory proper to the whole group. Regarding the ultimate units, or species, those which are most closely allied are likely to be found promiscuously associated in the same district and without the semblance of isolation. For example species of the Pruinosæ or of the Intricatæ with 10, or with 20 stamens, or with rose-colored, or with yellow anthers are found growing within a few feet of one another, and may cover common districts of several hundred square miles. In these cases, while it is the number of stamens or color of anther which first attracts attention, other specific characters exist which adequately distinguish the species. As an example of promiscuous association, the vicinity of Albany may be pointed out, where the five species of Intricatæ heretofore found in New York state grow in a small area. In Ontario we find twenty-five species of Tomentosæ, many of them growing very close together. In the distinctly southern group Microcarpæ we find the two species, *C. apiifolia* and *C. spathulata*, growing over the same areas, while the third and more distantly related species, *C. cordata* has a somewhat more northern range. In general, the reverse of Jordan's law would more nearly represent the distribution of American species of Cratægus.

Coming now to Orchidaceæ, I may say that I adopted the line of examination suggested by the form of Jordan's law; that is, I looked for pairs of kinds. I say kinds instead of species intentionally. The main problem should not be confused by the difficulty of agreeing upon a definition of species. What the evolutionist has to account for is not the definitions of systematists, but the multiplicity of hereditary types; he has to explain the antithesis between the uniformity which heredity seems at first to promise, and the diversity which actually prevails among organic things. A definition of species is demanded in taxonomy, but is somewhat less necessary in studies like the present. We do not require that the forms be related in some particular taxonomic sense; but only that they have different hereditary charac-

ters. In order to avoid complications I have used the word *kind* to designate such different types, instead of the words species, variety, etc., which have restricted technical senses.

I have sought for closely related pairs of kinds so made up that in each case no third kind stands between the members of the pair in resemblance. Such pairs I may call immediately cognate pairs, or for short, cognate pairs. A pair may consist of two species, two varieties, two subspecies, a species and a subspecies, a species and a variety, etc. It is assumed that such cognate pairs represent recent forkings of the phylogenetic tree; and that if we could collect all such cognate pairs in the vegetable kingdom we should have a representation of all the youngest forkings. Evidently their distribution would be very illuminating, for the youngest branches are on the average the least disturbed geographically, and the distribution of the members of these pairs would represent as accurately as we could ever discover it, the position of things at the moment when forking takes place. That is, we should have a geographic chart, more or less distorted it is true, of the origin of kinds. If the members of the pairs are universally, in the vegetable kingdom, separated from each other, then — as already explained — Mutation is excluded as a true cause of diversification of hereditary types in plants. For among several forms of isolation to which Mutation may conceivably give rise, and which are, therefore, not inconsistent with the mutational assumption, the one form of isolation to which it could never give rise is geographic isolation.

I repeat that I have examined only the broad geographical aspect of distribution and not at all the topographical, for which exact data are wanting. Let the reader recall the two stages of this general inquiry: my evidence belongs to the first of these. I present the following facts as a contribution towards an answer to the question, Is Mutation instantly excluded from a place among the considerable powers in evolution, by the broad aspects of specific distribution in plants? I have taken only one step. But this may be of some little importance, especially in view of the assertions concerning the distribution of plants which have been made, and in view of the lack of even broadly geographical statistics.

Evidence from the Family Orchidaceæ in North America

The American Habenarias have been given careful study in our laboratory. In addition to our own collections, those from several of the largest herbaria in the United States have been brought together. The species have been delimited with minute attention and then the distribution of each species, represented by the large amount of material assembled, has been recorded. Thus exceptionally full and reliable returns have been secured, which are available for the present paper.

H. ciliaris R. Br., and *H. blephariglottis* Torr., are a pair of perfectly distinct, yet extremely similar species. While instantly distinguishable in the field by their colors — the flowers of the former being yellow or orange, those of *H. blephariglottis* pure white — the dried specimens are separated only upon close inspection. The best distinguishing character is then the degree of fimbriation of the lip, which is considerably greater in *H. ciliaris* than in *H. blephariglottis.* No third species stands between them. They are spread together through the eastern United States. *H. ciliaris* is found in Massachusetts, Connecticut, New York, Ontario, Michigan, New Jersey, Pennsylvania, Ohio, Indiana, Delaware, Maryland, District of Columbia, Virginia, Kentucky, North Carolina, Tennessee, Missouri, Arkansas, S. Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, Texas. *H. blephariglottis* is found in Newfoundland, Nova Scotia, New Brunswick, all New England, New York, Ontario, Michigan, New Jersey, Pennsylvania, Ohio, Virginia and North Carolina; and if we include the southern form which may possibly be distinguished, the range is extended to South Carolina, Georgia, Alabama, and Mississippi. Whether we allow that the southern form is distinct or not is immaterial, since it does not stand between *H. blephariglottis* and *H. ciliaris,* and the latter species covers the range of both the northern and the southern forms of the other.

H. cristata R. Br., *H. chapmanii* Ames, and *H. ciliaris* R. Br., form a group of very closely related kinds. *H. cristata* is like a very small *H. ciliaris,* with a broader and un-clawed lip, petals oblong or somewhat obovate instead of linear, and a spur

shorter than the ovary instead of longer. *H. chapmanii* is intermediate between the others in perhaps every respect, and this fact, with the absence of any new character of its own, makes this species appear very like a hybrid. Its apparently local occurrence is in favor of hybridity. But allowing it to be independent, it forms a pair with *H. cristata* on one side, and with *H. ciliaris* on the other. On the other hand, removing the plants now grouped as *H. chapmanii*, because of suspected hybrid origin, we have left a very close pair in the two supposed parental types. On any disposition of the matter, the geographical ranges of the three kinds are found to coincide widely. The range of *H. ciliaris*, as above shown, extends from New England to middle Florida and Texas, and inland to Michigan, Missouri and Arkansas. That of *H. cristata* includes all the Atlantic states from New Jersey to Louisiana, with Pennsylvania, Tennessee and Arkansas added. Specimens of *H. chapmanii* have been seen only from northern Florida.

Habenaria psycodes Gray, and *H. fimbriata* R. Br. are a very close pair, with no intermediary. They are with some difficulty distinguished, yet statistical studies that I made upon them some time since convinced me that authors, including the most reliable authorities, are right in considering them specifically distinct. No one character can be relied upon to separate them invariably but all characters of each species fluctuate, so that any given part in one may run into the form characteristic of the other species. The balance of characters, however, is almost always decisive. The geographic ranges are very largely the same. Both are found in Newfoundland, Nova Scotia, New Brunswick, Quebec, all New England, New York, New Jersey, Pennsylvania, and North Carolina. *H. psycodes* extends further west, and *H. fimbriata* a little further south, as represented in the collections before me.

H. peramœna Gray, has for its probably nearest relative *H. fimbriata* — or possibly *H. psycodes* — with no species between. The three species mentioned, with *H. leucophæa*, form a group of close affinity. While *H. peramœna* is more widely distributed westward and southward (Ill., Mo., Ala.), and *H. fimbriata* much further northward, they occupy extensive territory together; *viz.*,

Pennsylvania, West Virginia, North Carolina, and Tennessee. If *H. psycodes* is substituted for *H. fimbriata* in the comparison, the geographic result has the same influence on the discussion.

H. orbiculata Torr. and *H. macrophylla* Goldie are so close that the plants of the two kinds have long been accepted by collectors and described by authors as of one species. The differences are at first sight slight, but are apparently constant and sufficient for distinction. The former species has a much greater range, which completely covers that of the latter. *H. orbiculata* extends from Labrador and Newfoundland westward through Michigan, and Minnesota, to British Columbia and Washington; and southward through New England, New York, and Pennsylvania to South Carolina and Tennessee. It is found in every district where *H. macrophylla* is found; viz., Newfoundland, New Brunswick, Ontario, Michigan, New England, and New York. The status of these two species is discussed by Ames in *Rhodora* for January, 1906, with illustrations of the flowers.

The difficult genus Spiranthes has lately been thoroughly studied by Ames, who has given the results in Orchidaceæ, Fasc. I, pp. 113–154. The abundance of material examined may be seen from the citations of specimens in the detailed statement of the distribution of each species.

S. cernua Rich. has for nearest allies, first, the variety (which some authors regard as a species), *S. cernua* var. *ochroleuca* Ames, and secondly the species *S. odorata* Lindl. *S. cernua* may be paired with either of them. *S. cernua* and *S. cernua orchroleuca* in the dried state can be separated with certainty by no macroscopic character. They may be distinguished by the seeds, however, *S. cernua* being polyembryonic.[1] Unfruited specimens being indistinguishable in the dry state, the exact distribution of each form may not be very precisely defined, but Rydberg in Britton's Manual gives the range of var. *ochroleuca* as from New Hampshire and Massachusetts to Pennsylvania and North Carolina. I myself have identified, as being unmistakably typical *S. cernua*, specimens from Massachusetts, Ontario, Iowa, and Georgia.

[1] See my notes on the embryology of the two forms in Rhodora **2**, p. 227 (1900) and **3**, p. 61 (1901). In *S. cernua* embryo formation takes place without pollination.

Thus the range of the species overlies that of the variety. Geographic isolation is wanting.

When we compare *S. cernua* with *S. odorata* we find again a very strong likeness. *S. odorata* is usually much larger in all parts than the former. The length of the scape relative to that of the leaves is greater in *S. odorata*, and its leaves are less strictly radical. Those not expert in the genus Spiranthes would often distinguish the two species with difficulty. They might be regarded as elementary species in de Vries's sense. *S. odorata* has been found in Virginia, Georgia, Florida, Alabama, Louisiana, and Texas, and its range thus coincides widely with that of *S. cernua*.

S. romanzoffiana Cham. and *S. porrifolia* Lindl. are very closely related species, which no other species approaches. The former is by very much the more widely dispersed, since it crosses the continent, while *S. porrifolia* is confined — according to specimens seen — within the states of Washington, Oregon, and California. *S. romanzoffiana* is represented in our records by many specimens from these same states, and there is therefore no general geographic separation in this case.

S. laciniata Ames and *S. vernalis* Engelm. and Gray are extremely similar but distinct species. The former is confined to Georgia, Florida, Alabama, Louisiana and Texas. *S. vernalis* occurs in all these states, but reaches far beyond this area.

S. beckii Lindl. and *S. gracilis* Beck are an immediately cognate pair of near affinity. The former grows in the Atlantic states from Massachusetts to Texas. *S. gracilis* covers the same range, but is also to be found further north and further inland. There is no geographic isolation.

Cypripedium pubescens Willd. and *C. parviflorum* Salisb. have had attention at this laboratory for several years, observations having been made in the field and in the herbarium, and collections of dried specimens having been received from many sources. Measurements indicate that there are two pronounced tendencies as regards size of flower. In life, the plants generally have an appearance of distinctness, and most field naturalists whose opinions have been asked, have maintained that the two kinds are specifically different. The manuals treat them so. Yet they

occasionally intergrade and perhaps can be regarded merely as subspecies. I have found them growing together in closest proximity. We have specimens of *C. parviflorum* from Ontario, British Columbia, New England, New York, New Jersey, Pennsylvania, Ohio, Indiana, Michigan, Wisconsin, Washington; and of *C. pubescens* from New England, New York, Pennsylvania, Ohio, Illinois, Wisconsin and Minnesota. The manuals extend the reported occurrence of both plants to Georgia. Thus the ranges of these two very closely allied kinds coincide over a very wide extent of territory. No other form in the world stands between them.

The genus Calopogon is confined to the eastern half of the United States (if we except the occurrence of *C. pulchellus* in Cuba), and comprises four close species and a variety, or five species. These species all come together and overlap in Florida. One, *C. pulchellus* R. Br., ranges from Newfoundland to Florida, Cuba, and Missouri, and geographically includes all the rest. *C. pallidus* Chapm. ranges from North Carolina to Florida and Alabama; *C. parviflorus* Lindl. from North Carolina to Florida; *C. multiflorus* Lindl. is confined to Florida. Here, therefore, are several pairs of cognate species not geographically separated.

Pogonia verticillata Nutt. and *P. affinis* Austin make a pair of very nearly related yet distinct species. The former extends from New England to Florida and west to Wisconsin and quite surrounds the other, a very rare species occurring sporadically in Vermont, Massachusetts, Connecticut, New York and New Jersey. Here again geographic isolation is wanting.

The conclusion from this examination of North American Orchidaceæ is that cognate pairs of kinds with uniform or widely coincident ranges are too numerous to leave any force at all in Jordan's law in its broad sense as regards this family in our flora. If one member of each pair was derived from the other member, or both were derived from a parent species, then, *as far as the geographic evidence goes, the new species may have originated in the same district with the old one*; *i. e. without geographic isolation.*

Concluding Remarks.

In concluding this paper I may make some remarks of a general character touching the whole problem.

First, we note that zoologists and botanists are rather distinctly opposed to each other in their views of the actual state of specific distribution. The suggestion is offered that zoologists may best discover the condition and interpret its meaning among animals, and botanists among plants. In no case is it safe to reason deductively from one kingdom to the other. In the factors affecting their evolution plants and animals differ vastly.

Secondly, in seeking for the laws of specific distribution we should first take the facts as we find them. We should agree to consider that in the absence of explicit evidence to the contrary, kinds now found in coincident ranges have been so situated from the beginning. In any given cases this assumption may or may not represent the truth, but we have no right to postulate movements in the past, of which there is no certain evidence, in order to save a preconceived theory. We may call such hypothetical migrations into being, in a strictly limited number of cases, upon a reconsideration, if from a first examination of the unmodified facts some law emerges so strong and compulsory that the few exceptional instances must somehow be brought into accord with it.

In the third place, if I may express my personal impression of the matter with regard to plants, it seems to me that the study of specific distribution in the vegetable kingdom is not likely to be unfavorable to Mutation, regarded as a method, but perhaps not the sole method, of evolution. It is true that in examining the distribution of species of plants, one encounters an effect which seems to be connected with geographical distance. We often find that a species of wide distribution exhibits slightly different phases in different divisions of its range. These phases are sometimes too subtle for definition and pass into one another by degrees, yet are evident to students of particular groups. Such cases do not look like the work of Mutation. They exemplify that which, to conceal ignorance of causes, may be termed a geographic effect.

But this aside, the indications seem to me to be that a good many instances sustaining the notion of mutative origin will be found among plants. It is not to be expected that the number of such cases will be *relatively* large. On the assumption of periodic Mutation as the origin of species, with competition between associated mutants and the survival of those mutants best fitted for existence in the original habitat, and the spread of mutants with new capacities into areas or habitats not open to the parental species, we should expect to find as a rule a single species occupying a given territory or ecological footing, and related species in separate, neighboring areas or habitats; though it is evident that mutants instantly endowed by Mutation with physiological or chronal isolation might continue to exist side by side with the parental species or with sister mutants if there were no active vegetative competition between the associated stocks. As a matter of fact, in many species of plants competition for subsistence between individuals of the same parentage is practically absent. Unification of congenital mutants may be brought about by continued interbreeding. This would eventually destroy the geographic evidence of Mutation in any given case. But in such amalgamation the effects of Mutation may not be destroyed; for new characters may during amalgamation be perpetuated in full force. It is single characters, rather than constellations of characters, with which the Mutation Theory is primarily concerned The number of cases of association of closely related species resembling recent mutants, in proportion to the number of cases of geographic or topographic segregation of closely related species would depend upon the balance between the activity of Mutation on the one hand and the operation of the forces tending to isolate or to amalgamate the products of Mutation on the other. If mutative periods are far apart in most species — and stability of the organic world may preclude great frequence — while the segregating or amalgamating powers are constantly at work, then the occurrence of the social condition indicative of Mutation may be expected to be relatively infrequent.

In order to use geographical evidence effectively against the Mutation Theory, its opponents must show that the social condition of closely related forms is, to use President Jordan's words,

"virtually unknown." In the vegetable kingdom this is likely to be an arduous task. The indications are that the adherents of Mutation will be able to bring forward enough cases of social distribution to render phytogeographic weapons useless in the attack upon this Theory.

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THE COINCIDENT DISTRIBUTION OF RELATED SPECIES OF PELAGIC ORGANISMS AS ILLUSTRATED BY THE CHÆTOGNATHA.

CHARLES ATWOOD KOFOID

No small part of the diversification of the organic world has taken place in the open sea. Whether we accept the view that the littoral and abyssal faunas are derivatives of the pelagic, or regard the latter as secondarily derived along many lines from the organisms of the shore and bottom, the fact remains that many groups have undergone great diversification both in the specific and in higher categories in the pelagic habitat. Illustrations of this process are to be found in the diatoms, the Protozoa (notably the Foraminifera, Radiolaria, Dinoflagellata and Tintinnoina), in the Scyphomedusæ, Siphonophora, and Ctenophora, Ostracoda, Schizopoda, Amphipoda, Decapoda, Heteropoda, Pteropoda, Cephalopoda, and Tunicata and certain families of fishes. The Nemertini, Annelida, Rotifera, Holothuroidea and the Hemiptera are sparingly represented. One class, the Chætognatha, are exclusively marine and pelagic, and their affinities are with the more primitive types of invertebrates. It seems probable that their entire evolution, or at least their generic and specific differentiation has taken place in the marine habitat. Their present distribution is therefore of prime interest because of its bearing on the relation of isolation to the origin and preservation of species.

Barriers are far less in evidence in the environment of the pelagic fauna than in that of the shore or of the land. A few instances in limited regions along the margins of great ocean currents as, for example, along the edges of the Gulf Stream or in horizontally stratified waters, there are abrupt transitions in temperature, but in the main the changes in temperature, illumination, density, and substances in solution or suspension, are so gradual that zoological provinces are delimited with difficulty and mainly in terms of temperature, on the high seas away from the influence of

shore conditions. In a large and somewhat vague way isotherms and isothermobaths constitute the barriers of the sea. Many, and in some groups, most of the pelagic species are wide-ranging, found in most seas, through a greater or less range of temperature. The pelagic fauna has thus a considerable cosmopolitan element and part of the differences which result in the contrasted poverty and richness of pelagic fauna are due to changes in the *numbers of individuals* and in the proportionate representation of the various components, as much as, or even more, than to *restrictions in the distribution of species.* In so far as the species of any group of related organisms establish themselves throughout a wide, coincident or overlapping range, in like degree isolation becomes problematical as a factor in the origin of new or preservation of old species.

Our knowledge of the horizontal and vertical distribution of pelagic organisms is lamentably incomplete and partial, and no less so of the Chætognatha than of other groups. Fowler (:06) calls attention to the fact that he finds no published record of a single *species* of that group between 160° E and 80° W, nearly the whole of the Pacific Ocean! Unfortunately no report was published on the Chætognatha of the Challenger Expedition and the results of later surveys have not yet appeared. We find, however, an excellent summary of the known distribution in Fowler's (:06) report on the 'Siboga' collections, based largely on his Biscayan investigations, Fowler (:05), and the work of Doncaster (:03) on the Maldive and Laccadive fauna, of Aida ('97) on that of Japanese waters, of Steinhaus ('96) and Strodtmann ('92) on collections from the Atlantic, and of various recorders in the lists of the *Conseil permanent pour l' exploration de la Mer,* from the waters of Northern Europe. The data thus assembled by one whose critical knowledge of the species has enabled him to sift out synonyms and eliminate probable errors, are far from being adequate to give a complete or satisfactory presentation of the distribution of Chætognatha in the seas named. They are, nevertheless, of sufficient fulness to afford a basis for the consideration of the extent to which isolation of species prevails in this typical pelagic group of organisms and to mark out clearly the necessity for additional data on vertical distribution and breeding seasons for a critical and final analysis of the problem.

It is the purpose of the present note to call attention to the important contributions which investigators of pelagic life might make to the discussion of this phase of the problems of evolution especially since monographers of pelagic groups are best qualified to judge of the degrees of affinity between the species of the genus and can determine whether the most closely related ones have a coincident or contiguous distribution. It is exceedingly desirable that future expeditions investigating the life of the high seas be equipped for a fuller analysis of the details of vertical distribution and that data on breeding seasons of pelagic species be included in monographs whenever available.

Genus Krohnia

This genus includes three species, *K. hamata, K. subtilis*, and *K. pacifica*. The first are two oceanic species of wide distribution, the last an Indo-Austral species of surface neritic distribution. The horizontal area of distribution of the first two species is largely coincident, *K. hamata* being known to extend to higher latitudes (81° N., 52° S.) than *K. subtilis* (60° N., 29° S.). As might be expected from its temperature relations, *K. hamata* is recorded from lower levels in the tropics than is *K. subtilis*. Data on this point are not very complete as *K. subtilis* is not an abundant species. The closing net catches of the Plankton Expedition indicate a maximum depth of 1500 m. for *K. hamata* and 850 m. for *K. subtilis*. The two occur together between 300 and 500 m. (37° N). The extent to which the vertical distribution of the two species overlaps cannot be determined from the available data. Fowler (:05) shows that the size of the individual of *K. hamata* increases with the depth in the Biscayan region. The young, that is, only small specimens, were taken above 500 fathoms and large ones with occasional small ones below that level. The sexual condition at different levels was not noted. The possibility of overlapping distribution is certainly present but contiguous distribution is by no means excluded.

Krohnia hamata is found in the mesoplankton of the Indo-Austral region, where *K. pacifica* is also found, but in surface waters exclusively. These two species were thus contiguous

rather than coincident in their distribution. There is thus little conclusive evidence of coincident distribution in the few species of *Krohnia.*

GENUS SPADELLA

The case of the two species of Spadella, *S. cephaloptera* and *S. draco* the area of distribution of the latter, which is a wide one, includes that of the former which is a neritic species from the northwestern coasts of Europe and the Mediterranean. They are both surface forms and their distribution is of the coincident type.

GENUS SAGITTA

The genus Sagitta as revised by Fowler (:06) includes twenty-one species. Their general horizontal and vertical distribution is shown in the accompanying table taken from Fowler's (:06)

			EPIPLANKTON									MESOPLANKTON						
			Atlantic Ocean					Indo-australian Ocean				Atlantic Ocean					Indo-australian Ocean	
	Neritic	Oceanic	arctic	sub-arctic	N. temperate	tropical	S. temperate	S. temperate	tropical	temp. N. Pacific Ocean	sub-arctic Southern Ocean	arctic	sub-arctic	N. temperate	tropical	S. temperate	S. temperate	tropical
ARCTICA	+	+	+	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.
BEDOTI	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.
BIPUNCTATA	+	+	+	+	+	+	+	+	+	+	.	.	.	+	+	.	.	.
DECIPIENS	.	+	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.
ELEGANS	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
ENFLATA	+	+	.	.	+	+	+	+	+	+	.	.	.	.	.	.	.	.
FEROX	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
FURCATA	+	+	.	.	+	?	.	.	.	.	.	.	.	+	?	.	.	.
HEXAPTERA	+	+	+	+	+	+	+	+	+	+	+	.	.	+	+	.	.	.
MACROCEPHALA	.	+	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	+
MINIMA	+	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.
NEGLECTA	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.
PLANCTONIS	+	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
PULCHRA	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
REGULARIS	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.
ROBUSTA	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
SERRATODENTATA	+	+	.	.	+	+	+	.	+	+	+	.	.	+	.	.	.	.
SIBOGAE	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
WHARTONI	.	+	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.
ZETESIOS	.	+	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	+
HAMATA	+	+	+	+	+	.	.	.	.	.	+	.	+	+	+	.	.	+
PACIFICA	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.
SUBTILIS	+	+	.	.	+	+	+	+	+	.	.	.	.	+	+	.	.	+
CEPHALOPTERA	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
DRACO	+	+	.	.	+	+	+	.	+	+	+	.	.	.	.	.	.	.

FIG. 1.—Geographic Distribution of Chætognatha, after Fowler (:06).

(Siboga) report. *S. bipunctata* is omitted by him from the Indo-Austral region in his text because of the uncertainty of its identification since it is quite similar to the young of several other species in the list. Of the twenty-one species, eleven, including *S. bipunc-*

tata, occur in the Atlantic, ten in the Indo-Austral, eight in Japanese waters, and two in the subantarctic, in the epiplankton. In the mesoplankton of the Atlantic eight species are found, and three in the Indo-Austral. In the larger geographical regions of the Atlantic we find coincidently in the epiplankton, in the Arctic, three species, in the subarctic five, in the north temperate, eight, in the tropical, five, in the south temperate, four; in the

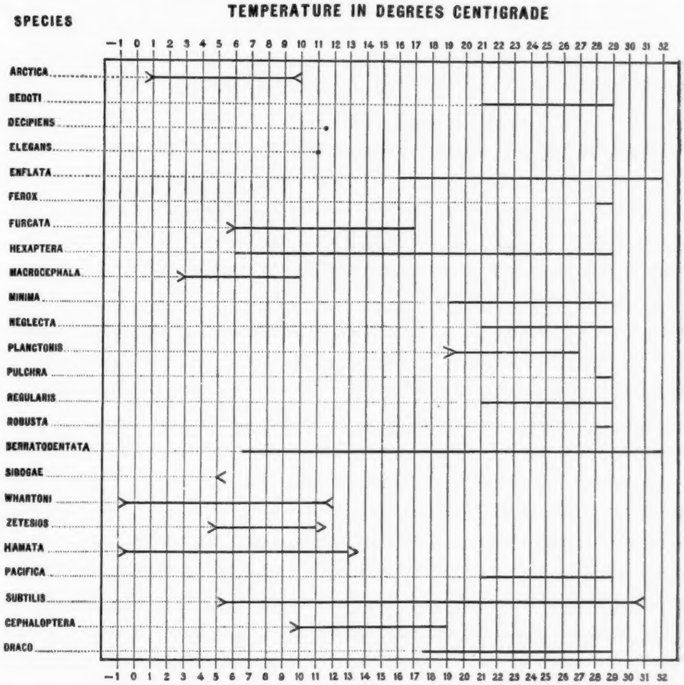

FIG. 2.— Distribution of Chætognatha with reference to temperature.

mesoplankton, two, eight and two species respectively in the subarctic, north temperate and tropical regions. In the Indo-Austral there are three species in the south temperate and ten in the tropical, with three in the mesoplankton of the latter.

The distribution of the species with reference to the temperatures at which they have been recorded is shown in the accompanying table from Fowler's (:06) report.

In the case of Sagitta the distribution is as follows:—

-1°	to	4° —	3 species
5°	to	10° —	7
11°	to	15° —	6
16°	to	20° —	6
21°	to	25° —	8
26°	to	32° —	11

This, in conjunction with the fact that some of the low temperature species belong to the mesoplankton of the tropics, indicates that the center of radiation of the genus has been in the tropics, or that specific differentiation has been relatively more rapid in that region than at the lower temperatures toward the poles.

These broader outlines of the distribution of the species of Sagitta are suggestive of a considerable degree of coincidence of distribution of species, it may be of closely related ones, and prompts to a closer analysis of their relationships and distribution.

The determination of degrees of relationship among species of a genus is a matter of inference from structural details for whose relative values we have no absolute standard. One's judgment is guided by the selection of characters on which classification is based, by experience in dealing with the specific analysis of the material, and subjectively, by the conception of species which one entertains. It is obvious that species differentiated by the slow accumulation of minute fluctuating variations would offer in their modified structures, some clue to the distance of their removal from the parent stock, or from each other. On the other hand the elementary species arising by mutation from *Œnothera lamarckiana* may be regarded as genetically equally related to each other or to the parent stock, but if we base our judgment of the degrees of the relationship which they exhibit solely on the structural characters which distinguish them, we would be forced to conclude that there was considerable disparity of relationship among them. The mutation theory admits a wider latitude in estimating the relationship of species than does the unmodified Darwinian point of view.

We have, however, in Sagitta only the result, and not the process of specific differentiation with which to deal, and are therefore

forced to depend solely upon structural resemblances for the determination of specific relationships.

The species of Sagitta are distinguished, among other less quantitatively expressed characters, by (1) size, (2) ratio of tail to total length, (3) number of jaws, (4) number of anterior and (5) posterior teeth. An analysis of Fowler's (:06) specific diagnoses reveals three groups of related species within which couplets of most closely related species may be noted.

The first of these, the *serratodentata* group, includes five species: *S. serratodentata*, a eurythermal cosmopolitan species with little tendency to sink to deeper waters in the tropics; *S. bedoti*, a neritic surface species from Indo-Austral waters; *S. ferox* and *S. robusta*, neritic and surface species from the Malay and Maldive Archipelagos; and *S. sibogæ*, taken only in hauls from deep water in the Malay Archipelago.

The following table of quantitative characters of the species taken from Fowler's records serves rather to indicate their close resemblance than to differentiate them. Other characters such as proportions, form of the eyes and teeth, assist in diagnosis.

Serratodentata Group.

Species	Length in μ	Tail in % of total length	Jaws	Anterior teeth	Posterior teeth
serratodentata	5–14	28–36	5–7	8–9	16–22
bedoti	13–20	21–28	6–7	8–10	17–29
sibogæ	9–20	21–33	5–7	7–10	16–22
ferox	10–20	29–36	5–6	6–10	9–14
robusta	10–14	25–33	5–7	6–9	10–15

The quantitative characters of the table in conjunction with others not included, suggest that the wide ranging *S. serratodentata* may be the ancestral stock of the couplets *bedoti* – *sibogæ* and *ferox* – *robusta*, or more nearly related to that stock than the couplets named.

The 'Siboga' lists indicate that these five species occur in the waters of the Malay Archipelago, but *S. sibogæ* only in collections from the deeper waters. The other four, however, are found together repeatedly in collections from the surface. In the 65 collections in which *Sagitta* occurs all four species appear in 27, three of them in 27, two in 9, and one in but 2, the average percent-

age of coincidence 80%. Of the 65 collections 55 were made at the surface. Four of the five species thus have a coincident distribution, including the mostly closely related couplet *ferox-robusta* and the very closely related *S. bedoti* and *S. serratodentata*. The *bedoti-sibogæ* couplet appear to have a contiguous distribution in the upper and lower levels, respectively, in this region.

A second group of species which show considerable resemblances to each other are *S. hexaptera*, an oceanic, stenohyaline, eurybathic, and eurythermal form; *S. enflata*, a warm water form of wide distribution in the epiplankton of warm-temperate and tropical seas; and *S. pulchra*, a neritic surface form from the Malay and Maldive Archipelagos.

The accompanying table indicates the relationships of the three species of the *hexaptera* group as suggested by the quantitative characters.

Hexaptera Group.

Species	Length in μ	Tail in % of total length	Jaws	Anterior teeth	Posterior teeth
hexaptera	15–70	20–25	6–8	3–4	2–7
pulchra	9–22	18–27	5–7	6–9	10–15
euflata	22–26	16–22	7–9	7–10	12–17

An examination of the 'Siboga' lists shows that the three species occur together in 24 catches, two in 26, and but a single one in 26, the percentage of coincident occurrence being 66%. The most closely related couplet in this group is *pulchra-enflata*, the former a neritic, the latter an oceanic species. These two occur together in the Maldives and also in the 'Siboga' collections, where *S. enflata* is one of the most abundant species. It is found in every one of the 34 collections in which *S. pulchra* appears. Of the 34 coincident occurrences 29 are in surface collections. These three related species have here a coincident distribution and *S. hexaptera* and *S. enflata* have a common distribution over a much wider area.

A third group of related species includes *S. bipunctata*, and two couplets of most closely related species, *furcata-planctonis* and *neglecta-regularis*. Published records indicate that the first named species is a cosmopolitan one of wide range. Difficulties attend its specific determination so that Fowler is of the opinion that it is possibly only an Atlantic neritic form not occurring in Indo-Pacific waters.

The members of the first couplet, *furcata – planctonis*, are Atlantic species, the former of wide distribution, 51° N. to 7° S., in the epiplankton of colder waters (17°) and the mesoplankton of the tropics. The latter occurs only in the epiplankton of the tropics. This couplet of most closely related species has a contiguous rather than a coincident distribution. The distribution of both, however, is overlapped by that of the very closely related *S. bipunctata.* The degrees of relationship as suggested by quantitative characters may be inferred from the accompanying table.

Bipunctata group.

Species	Length	Tail in % of total length	Jaws	Anterior teeth	Posterior teeth.
bipunctata	12–20	21–25	8–10	4–7	8–18
furcata	21–27	22–24	6–7	4–6	9–10
planctonis	17–23	23–26	7–9	6–8	9–10
neglecta	5–10	26–40	5–8	4–6	9–12
regularis	4.5–7	28–40	5–7	2–4	4–6

The members of the second couplet of most closely related species, *S. regularis* and *S. neglecta,* are both surface neritic forms of the Malay Archipelago and Japanese waters. *S. regularis* is neritic also about the Maldives and it may be that Doncaster (:03) overlooked the very similar *S. neglecta* in the collections from these waters. The distribution of these two most closely related species is thus widely overlapping, if not indeed coincident.

The distribution of pelagic organisms, as illustrated by the Chætognatha thus affords several probable instances of the isolation of the members of couplets of most closely related species by isotherms or isothermobaths. This isolation is similar in many of its aspects to that so often found between terrestrial species. It may well be that isolation has been an essential factor in the differentiation of the members of these couplets. Even more general, however, in the pelagic world and among the species of this same group is the phenomenon of the coincident occurrence of couplets, and of larger groups, of most closely related species. We have now no evidence of differential seasons, temperatures, or levels at which breeding might occur in these closely related species. Should these differentials ultimately prove to be absent

we would be forced to conclude that isolation has had no part in the origin, differentiation, and continuance of these related species.

In *Dagitta bipunctata* Miss Stevens (:03) has described a method of close fertilization. As yet we have no light on the extent of its occurrence in other species where the presence of enlarged seminal vesicles and external male parts affords suggestive though not conclusive evidence of external and presumably of cross fertilization. Should all species of Chætognatha prove ultimately to have close fertilization we would have in this a most effective means of isolation.

The apparently wide-spread phenomenon of coincident distribution of related species among pelagic organisms appears to cast some doubt upon the universality of the operation of isolation in the evolution of species as originally maintained by Moritz Wagner ('68) and recently revived by President Jordan (:05).

The contrast here afforded also raises the question whether the two types of 'species' really belong fundamentally to the same category or not. Are those with contiguous distribution, and also many of the geographical species and subspecies of land vertebrates, of a standing exactly equivalent to that of those having a coincident distribution? Are, for example, *S. furcata* and *S. planctonis* merely the extremes of an environmental series beginning in the warm surface waters and ending in deep waters of lower temperature? In other words are they the result, in part at least, of the pressure of the environment? A statistical study of the distribution and variation of such a pelagic couplet and a comparison with a similar study of a couplet having a coincident distribution would be most instructive in indicating whether or not any distinction exists between 'isolation-environmental' species on the one hand and 'selection-mutation (?)' species on the other. Are intermediate forms equally absent in both types of couplets? Is variation similar in kind and in distribution among the individuals of the two types? Above all will the individuals of the isolated couplets maintain their specific integrity if their environments are transposed? And finally will the species with coincident distribution exhibit any greater specific stability under environmental changes than will those produced by the agency of isolation?

Investigators of pelagic organisms have been morphologists so

generally, rather than primarily systematists, that the bearing of the data of the geographical distribution of the organisms with which they have been dealing, upon the broader problems of evolution has been somewhat neglected. It is greatly to be hoped that the life of the sea, primitive, ancient, diversified as it is, may yet shed some light upon the problems which this brief paper can do little more than suggest.

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THE ATTACHED YOUNG OF THE CRAYFISH *CAMBARUS CLARKII* AND *CAMBARUS DIOGENES*

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A REMARKABLE fact in the life history of the crayfish is that the young associate with the mother for many days after leaving the egg, being at first firmly fastened to her and later going back to her for protection until finally quite independent.

As pointed out in *The American Naturalist*, March, 1904, *Cambarus affinis* molts twice while fast to the mother and leaves her only in the third stage. Some facts as to the character of this incipient family life in an American Astacus from Oregon will be given in another communication. The object of the present note is to describe the association of parent and offspring in two more species of Cambarus and to compare this with what is found in *C. affinis* and in Astacus. The illustrations are all of *C. clarkii.*

The young of *C. clarkii* were obtained from eggs laid in confinement by adults shipped from New Orleans, November 18, 1904; some 18 out of 61 surviving the journey. Two of these active, prawn-like and brilliant red crayfish, one male and one female lived in a shallow sink of warmish water during the winter and by March 25, 1905, the single female had the abdominal basket full of many very small and very dark-colored eggs. These eggs were already in the stage H of Reichenbach but differed from that in having the abdomen larger. Each egg was about 1½ mm. in diameter and partook of the exceptionally vivid coloring of the adult, the large oil-like yolk drops being wine colored instead of yellow as in *Cambarus affinis.*

When received in November, three of the females examined had only minute yellow eggs in the ovaries and no sperm in the annuli, while the males had small testes but yet mature sperm in the vasa deferentia. It would thus appear that the season of conjugation may be late autumn or winter, and that of laying early spring, but this can be determined only by observations in the field.

By April 17 the eggs had become coated over with a dark deposit, but the embryo within was far advanced and easily escaped when pressure caused the egg case to spring open. With Zeiss 2. A. it was evident that the embryo was clothed in a loose cuticle, or cast off shell, which loosely invested the tips of the first and second antennæ, the chelæ, the walking-legs, the abdomen and thorax as well as the ends of the gills when torn out of the gill chamber.

These embryos were now essentially the same as when they hatched three days later. The eyes were almost sessile and with the pigment restricted to a narrow crescent and this pigment reflected yellow light but appeared black by transmitted light. The yolk was still a large dark mass of saddle-bag shape. The tips of the fourth and fifth legs were strangely bent back like hooks while the tips of the claws of the chelæ did not as yet seem to be recurved. All over the body the extremely dark crimson pigment cells again emphasized the agreement of embryo and parent in intensity of coloration.

But the detail of anatomy of the telson was the most important character for understanding the subsequent attachment of the young to the parent. The abdomen ended in a simple, flat, rounded telson that bore a row of simple spines along its posterior edge as seen with 2. D. in figure 3. The spines were fourteen or fifteen on each side symmetrically placed right and left, and a group of seven or eight of them on each side, near the median plane, seemed to push off the loose cuticle, which on the middle plane, was close to the body. The spines, or better, papillæ, were highly refractive and clear except that some showed granules and some vacuoles in their homogeneous contents. Some of them had small protrusions at the tips as if paste-like material had extruded from within.

The spines in the special group, right and left, converged, arched over, met and seemed grown together. On the animal's left the spines 7 and 11 were grown together at their tips while 8 and 10 seemed fused together at the tips into one continuous arch and the same was true of 9 and 12. With higher power, 4 mm. 4.45 comp. oc., tufts of fine threads, or fibrils were seen diverging from the tips of many spines to pass, posteriorly, often beyond the tips of other spines. Some of these threads passed out to the

loosened cuticle and seemed fastened to it. On the right of the specimen fine wavy lines suggested secreted films rather than fibrils.

As will be seen later these specialized spines are glandular structures that make the telson adhere firmly to the cast-off cuticle and thus make possible the "telson thread" of the hatching larva.

The small number of spines so grouped, together with the fact that the telson of earlier embryonic stages is incised on the middle of the posterior edge suggests that these 7 or 8 spines may be comparable to the 7 or 8 spines seen on each side of the incised telson of the lobster embryo (Fig. 72; Herrick; The American Lobster) before it molts at the time of hatching and is in a stage which Herrick compared to a protozoea, or other early larva. On this basis a very remote ancestral state has been retained to the extent that its spines have been applied to the new use of attaching the larva to its cast cuticle.

Before speaking of the hatching larvæ it must be recalled that all crayfish eggs are fastened to the pleopods of the mother by a hardening mass whose origin is somewhat in dispute. In *C. clarkii* the pleopods of the mother were so translucent that the transverse striation of the muscles was seen through the exoskeleton and with 2. D. the gland cells that are supposed to take part in fixing the eggs to the pleopods were seen as polygonal areas of secretion droplets separated by clear lines.

All over the bases of the pleopods these areas were massed together but the terminal part had them arranged in transverse bands that crossed the anterior face and extended into the sides but left the posterior face without glands. On the bands anteriorly were small tubercles each with a number of tubes passing from the glands to the surface and near these were some short, sharp setæ which occurred again at the tips of the pleopods.

While it is possible that these sharp setæ act in pricking the eggs and liberating an adhesive material as claimed by Williamson for crab's eggs, and that the glands of the pleopods have nothing to do with fastening the eggs, yet this seems very improbable, as the eggs are fastened to a large mass of material similar to the egg case and stalk and which binds all the long plumose setæ together and is most probably the product of the pleopod glands.

The small first pleopods also had glands and setæ like the others but were more colored with large, arborescent, red cells.

When fastened to the mother each egg was in a remarkably elastic case which had a rough, dirty outside layer and a clear inner layer containing the same microscopic droplets seen in *C. affinis* and similar to the droplets coming from the pleopod glands. Each case was continued on one side as a long stalk that in turn was continuous with the hardened secretion binding together the plumose setæ along the edges of the pleopods. The stalk was hollow though flat and wide and was a continuation of the dirty outer layer of the egg case, separating from the inner layer on one side to form a large hollow bell or tent.

Between the egg and the egg case was a variable amount of coagulum showing fibrils in it.

By April 17th some of the larvæ had hatched while others were not yet out of the egg cases. The young, figure 1, had the usual embryonic look of crayfish at hatching; a huge swelling of the head region owning to the presence of much yolk there; a weak development of the locomotor part of the head-thorax so that the five pairs of weak legs all arose posterior to the middle of the head-thorax; a weak, down-bent abdomen of little use in locomotion; eyes almost sessile and of little size or perfection. These larvæ were transparent and showed the heart beating rapidly and the scaphognathites rapidly baling the water out of the gill chambers. The dark area in figure 7 represents the dark red yolk mass; and the scattered dots, the aborescent pigment cells that were thickly scattered over the head-thorax and abdomen with but few upon the third maxilliped, base of antenna, three basal segments of the antennule and some few segments of the periopods.

Normally the larvæ remained upon the mother and did not move about, and when pulled off and put on the bottom of the dish they could not stand up but could progress by lying upon the side and flapping the abdomen.

At hatching, figure 1, the young were so weak they would have dropped to the bottom but for the "telson-thread" which is the cast off cuticle pulled out into a thread or band and fastened at one end to the telson of the larva by the special telson spines described above and at the other end to the inside of the egg case. As the egg case still remains fast by its stalk to the mother the larva is hung suspended from the mother till able to use its claws

and obtain a hold by them to the egg stalk or to parts of the material covering the plumes of the pleopods.

In hatching the larva escapes not only from the egg case but from its loose cuticle and this cuticle, where it covers the abdomen, is pulled inside out, but leaves the telson spines fast as before to the inside of the cuticle over the tip of the telson. The cuticle is so strong that larvæ may be picked up by the telson thread and their weight does not break it even when hanging in the air.

The attachment of the cast cuticle to the inside of the egg case seems to be an indirect one; apparently the larval cast cuticle is in some way fast to the egg membrane and that in turn adherent to the inner of the two layers that makes the egg case, but this was not definitely seen. In many eggs the embryo when young lies upon the side of the egg near the stalk and we suspect some relation between the region of fertilization and of stalk formation. Later, when the embryo hatches, it goes out back foremost through a crack in the case opposite to the stalk. In the old embryos the tip of the telson is carried forward to near the eyes and not far from the stalk of the egg case and in that same region of the egg is found the connection of egg case to embryonic cuticle. Possibly there may be some common factor, as gravitation, that determines at fertilization the position of the embryo, the place for formation of the egg stalk and the connection of egg case and larval cuticle.

The part played by the special telson spines in holding the larva fast to the telson thread is shown in figures 2 and 4, which show how the wrinkled telson thread is connected to fibrillar material, fastened to and interlocked with the long, curved and arched spines. In passing from the condition shown in figure 3 to that in figure 4 the cuticle over the abdomen has been pulled off and turned inside out and is now free from the larva except where held by the material furnished by the glandular spines.

When the young get hold of the mother pleopods with their claws they soon break the telson thread, but a short end of it long remains fast to the telson and the main mass still recognizable is fastened to the egg case.

In this first larval stage these young crayfish were about $4\frac{1}{2}$ mm. long from tip of telson to a point between the eyes where the rostrum turned down close against the head and was concealed between the eyes. The antennæ were $1\frac{1}{2}$ mm. long.

The accompanying camera sketches from specimens hardened in Worcester's liquid show the generally imperfect state of the appendages of the first larva, which lived for a few days an inert embryo-like existence fastened to the mother and not eating but only rapidly aerating and circulating its blood as the yolk was being transformed. The first antenna, figure 8, has only four segments in its exopodite and in its endopodite and agrees with most of the other appendages in being devoid of setæ. This bareness of the appendages of the first larval stage was first pointed out in the English Astacus by Huxley and seems common to all crayfish larvæ in their first stage. In place of setæ there are but a few spinules at the tips of the first antenna and on the basal segment there is a small ear-pit; but as yet the entire appendage would seem of no use as a sense organ.

The second antenna, figure 9, has only 24 segments in the slender part of its filament, beyond the three large broad segments, and the exopodite scale bears a blunt process and a row of few, sharp spines. The tubercle upon which the nephridial canal opens is, as in all young crayfish, proportionally very large.

The mandible, figure 10, has a smooth edge with no teeth and is probably not used. The first maxilla also, figure 11, is very simple and probably of no use.

The second maxilla, on the other hand, figure 12, bears the large scaphognathite which is very active in removing water from the gill chamber. The setæ along the edges of the scaphognathite, though represented in the figure as smooth, were in reality, under 2. D., set with five side branches so that in this only actively moving appendage the setæ are present as plumes that would seem to be of use in striking against the water and in making the appendage fit more closely into the passage leading out of the gill chamber.

The three maxillipeds, figures 13, 14, 15, are strangely lacking in setæ except upon exopodite of the first where there is a row of sparsely plumose setæ. The gills begin as a large podobranch and a slender anterior arthrobranch on the second, figure 14, and on the third, figure 15, there are two arthrobranchs. The projecting lobe at the base of the epipodite, or lamina bearing the filaments of the podobranch, is conspicuously large in all larval crayfish and here bears a few, acicular setæ. Probably these

lobes and setæ aid respiration in making the inlet water more free from dirt.

The chelæ, figure 16, are long and strong but as yet not specialized as cutting organs. The tips of the claws are recurved as Huxley first found them to be in the English Astacus so that once shut upon a penetrable mass they could scarcely be loosened by the larva, figure 17. By means of these locking tips the young become fastened to the egg stalks and to the hardened secretion on the mother's pleopod setæ so that they probably remain fixed in one spot all the time they live in the first stage. The simple, acicular setæ seen along the edge of the claw, figure 17, may possibly aid in tactual reflexes to enable the larva to shut its claw on suitable substances.

The next two pairs of legs are very like the chelæ, but more slender, short and weak.

The fourth leg, figure 18, with no claw, has its arthrobranchs much reduced, the anterior having but slight protuberances to represent lateral filaments and the posterior being quite smooth.

The fifth leg has no gills at all associated with it; the pleurobranch of Astacus being absent not only in the adult Cambarus but in the earliest larva here as well as in *C. affinis* and, as long ago determined by Faxon, in *C. rusticus*. The branchial formula is thus the same in the larvæ as in the adults.

On the abdomen the appendages have the incompleteness of all crayfish larvæ. The first pair are not begun and the sixth pair are forming under the exoskeleton within the base of the telson. The other four pairs are very small and apparently quite useless structures each projecting towards its fellow crosswise under the abdomen and with the endopodite more anterior and the exopodite more posterior. As seen in figure 19, the endopodite is somewhat the larger and both endopodite and exopodite are very simple and show but slight suggestions of spines at their tips.

The telson, figure 2, is a simple, elongated, flat plate showing within its clear substance radiating lines ending at the marginal spines and also the outlines of the long exopodites of the sixth pleopods lying along on each side of the rectum and anus. On the ventral side, figure 1, the base of the telson is quite protuberant over the part of the enclosed pleopod that will be the exopodite.

In larvæ that have been in the first stage a few days and are about ready to molt it is obvious that the radiating lines in the posterior part of the telson are the glands secreting the setæ which will replace the marginal spines at the next molt. In a prepared section of the posterior part of the telson of such a larva, figure 5, the old cuticle is separated from the epidermis by a space across which the tips of the forming setæ pass toward the hollow bases of the old spines. Each old spine has a new seta beneath it but as there are also other setæ the second larvæ will have more setæ than the first had spines; the long plumes, however, figure 7, are slightly fewer in the second larvæ than the spines in the first.

Each developing plumose seta seems a flat plate ending in a fine central thread and with its edges frayed out in short fine threads. The base of each is deep within the epidermal ingrowth that forms the secreting gland. Each gland seems a row or rod of cells, indicated by large nuclei in a common protoplasm in which no cell walls were seen. The longitudinally striated base of the plumose seta forms the axis of the rod of cells. The space between the radiating glands was in part occupied by blood, staining, like the setæ, yellow, while the nuclei were red in borax carmine and orange G.

Similar, but less developed rods of cells were also seen in sections of the internal buds of the sixth pleopods where they were forming plumose setæ that projected into a bag surrounding the pleopod.

By April 24th, when some of the larvæ had begun to molt, it was evident that something was abnormal, as some larvæ in both the first and the second stages fell away from the mother and died. The mother also died, April 28th. The hatching was prolonged more than is probably normal so that many first and second stage larvæ were found side by side for a few days. Some of the young in the second stage remained with the mother for a few days but made excursions away from her and again returned as was the habit for the second stage in *Astacus leniusculus*, but it is not certain that this was normal in *C. clarkii*. While upon the mother these young held firmly with their chelæ, but they let go when the dead female was lifted out of the water. When upon the bottom of a dish they were able to stand up and walk feebly, and after a day, they swam backwards on their sides by flapping

the abdomen. They tended to climb over one another and one held so fast to a dead fellow that it could be shaken loose only with difficulty. They also climbed up on to the dead female and on to a piece of Canton flannel where they held fast by their chelæ for a time and then got down and swam actively if disturbed by a pipette.

Though the larva in the second stage may thus go away from the mother it doubtless returns even into the third stage as Faxon records finding upon the abdomen of museum specimens larvæ with characters evidently of the third stage.

The second stage young, figure 6, were still so translucent that in the abdomen the digestive tract and the ventral ganglia could be plainly seen.

In *C. affinis* it was noticed that the young, in passing from the second to the third stage, was suspended from its cast cuticle by an anal thread which bound its anus to that of the cast off cuticle and as the claws of that cuticle still held fast to the mother the young was prevented from dropping away from the mother till able to take hold again with its new claws. In *C. clarkii* the same arrangement may prevail though it was noticed only in two larvæ that died just after molting. In these there was a long thread that issued from the anus and, passing down through the hollow cast off cuticle of the abdomen, was fastened at the bottom of it to the flat telson. By the strain of the anal thread the cast off abdominal cuticle had been telescoped; the old telson being dragged up against the collapsing rings of the cast cuticle. As in *C. affinis* this anal thread was only the cuticular lining of the intestine not cast off entirely at the same time with the external cuticle and thus serviceable in binding the larva to its old shell. If this tardiness in casting the lining of the intestine is normal in *C. clarkii* it would seem a useful means of holding the young to the mother when soft and helpless at molting time, provided the young molts while upon the mother, which is probably the case even if it has some freedom of motion in the second stage.

In contrasting the second stage, figure 6, with the first, figure 1, we find an increase in size, the body being now 5½ mm. long with antennæ 3 mm. long, and some advance in the proportions of the body and in the perfection of the limbs. While the head-thorax

still contains much yolk it is less swollen and more elongated while the abdomen is relatively larger and it is more useful as its telson bears a fringe of setæ.

The limbs are changed but little, yet they now bear some setæ though these are too small to show under low magnifications, figure 6. The rostrum is still triangular, but sharp, and though it is still bent down between the eyes it can be seen from a dorsal view and also from a side view, figure 6, where its base is visible near the eyes which are now decidedly stalked.

The first antenna had six segments in its exopodite and in its endopodite and the former bore five sense setæ, three on the terminal and two on the fifth segment. The ear was a wide open cavity with three or four finely barbed setæ along its external border.

The second antenna now had a long spine and a row of 19 or 20 plumose setæ on its scale and its filament contained 34 segments some of which seemed to be dividing.

The mandible edge was now no longer smooth but had six or seven teeth on its free edge and three above the palpus.

The spines at the tips of the chelæ, figure 20, stood at about right angles and were but slightly recurved. Along each edge of the claws was a row of peculiar spines having a thick edge and a narrow blade, figure 20, which tended to be cracked or striated across its length. These cutting or rasping spines are a specialization not found in the first stage when the claws are used only as hold-fasts.

On the abdomen no new appendages were found but the four pleopods present were now well provided with plumose setæ. The telson of the second stage, figure 7, compared with the first stage, figure 2, shows a great increase in size and the addition of a row of barbed setæ in place of the simple marginal spines. The sides of the telson protrude so much where the enclosed sixth pleopods have enlarged that its margin is somewhat three lobed; all the setæ are upon the middle or posterior lobe, and are symmetrically placed right and left. In the middle line there are no setæ; and right and left they begin short and suddenly reach the greatest length and then, as seen in figure 7, are long enough to make an efficient increase in the length and area of the telson as an organ for striking against the water in swimming.

In the figure the dotted lines represent the enclosed pleopods and in them the radiating setæ glands in which are forming the plumes to be expanded at the next molt. Studied in life with Zeiss 2. D. these glands were long tubes from each of which projected a plume, the tip of which turned to one side in the space between the edge of the pleopod and the enveloping sac. In the same way the posterior end of the telson showed long tubular glands forming a set of plumose setæ to replace those already present. The tip of each new plume projected slightly from its gland into the hollow base of the existing plume, which would be cast off with the cuticle of which it is a part, at the next molting. All these setæ seen in formation in long tubes are richly barbed plumes that later come into use when suddenly exposed to the water at the next molt.

Only some five or six of these specimens of *C. clarkii* survived to change into a third stage, April 29 to May 1st, but these agreed with all known crayfish of the third stage in having a complete tail-fan, with both telson and widely expanded sixth pleopods together forming a very large area for resistance to the water and set all along the combined edges with the above long plumose setæ.

Though these few individuals seemed weak they both walked and swam easily. The color had now become a darker flesh-color from the crowding of red pigment cells, but the area about the stomach was lighter and on each side of the stomach there was a small, narrow, dark band representing the yolk.

As above stated it is probable that in nature the larvæ in the third stage remain with the mother for a time, and then gradually become entirely independent.

While the conditions seem to have been so unfavorable for *C. clarkii* that the young were weak and probably somewhat abnormal in their actions this was not the case with the young of another crayfish, *C. diogenes* Girard as kindly determined by Walter Faxon. April 8, 1906, ten females with eggs in late stages, three females without eggs and twenty-two males were obtained from Talbot Co., Maryland, by a collector who stated that they usually breed in May and are caught walking about in ditches.

The eggs were nearly black, or upon a few females dark brown, and of great size, being $2\frac{1}{2}$ to 3 mm. in diameter, while in *C. affinis* they are $1\frac{3}{4}$ to 2 mm. and in *C. clarkii* only $1\frac{1}{2}$ mm.

The young were hatching upon six of these females May 22nd and just before this an examination of the embryos showed a delicate loose cuticle over each tip of the chela, over the abdomen, and over the body, and an egg opened in strong sugar solution, and then put into water showed a cuticle swelling up all over the antennæ, the chelæ and the abdomen. But when carefully dissected it seemed that this cuticle was not a case over each appendage but rather that it was a large bag over the thorax, a side pouch over the abdomen, a large side pouch over all the pereiopods and a side pouch over all the gills. Probably, however, there are two thin membranes, an outer vitelline membrane of irregular form when stretched over the protuberant regions of the animal and an inner, real cast-off cuticle, that goes over each appendage; for some dissections showed the embryo inside a delicate spherical bag fastened to the inside of the egg case, and observations upon the hatching larvæ seemed to show them drawing out the limbs from separate envelopes.

At the end of the telson there were groups of spines fastened to the cuticle by refractive fibrillar coagulum. On each side a group of six spines arched over and connected very much as in *C. clarkii*, figure 3, and here the cuticle was thrust off further, while on the middle line it was close to the telson.

In one individual the actual hatching lasted forty-five minutes; the egg case cracked open opposite to the stalk and the embryo slowly "oozed" out back forward. During this process some movements of the legs were seen as well as a rhythmic pulsation of the lateral lobe of the liver lying close to the yolk mass on each side of the body, and swaying movements of the yolk mass. This tube was filled with yellow liquid for ten or twelve seconds and then grew narrow and white for about two seconds and again filled. It seemed as if the tube were contractile itself, but the yellow liquid may have been forced into it and so have caused it to distend. In either case the rhythmic filling would seem useful in aiding in digestion of the yolk, which was the only available food so far. Should it prove that the adult liver also rhythmically fills and empties it would be an interesting addition to the anatomical and physiological evidence advanced by H. Jordan (Pflüger's Archiv, 1904,) to show that the 'liver' is the chief organ for absorption as well as secretion.

As soon as out of the egg case the larva began to kick its legs and in a few minutes the scaphognathite slowly moved, stopped and began again, finally establishing a rapid rhythm. On adding carmine, the currents made by the scaphognathite were visible and its movement seemed comparable to a scooping motion of a hollowed hand, the fingers downward, thus forcing the water through the dorsal part of the respiratory passage as the fingers closed the lower part and then rising up to close the upper part and prevent a back set of water into the passage way.

Once out of the egg case the larva was still fastened to it by a telson thread consisting of a short string from the telson spines to a large crumpled mass that seemed a cast off cuticle and lay just within the gaping egg case and was fastened to it, inside, by the intervention of an expanded membrane which may possibly have been the old vitelline membrane. This membrane was bound to the inside of the egg case by a few short fibrils over a round area smaller than the base of the egg stalk and often near it. Thus suspended the larva moved its legs weakly and now and then shut its claws and violently flapped its abdomen without breaking loose from the telson thread. Soon the larvæ became fast by their claws to the egg stalks or to the material on the plumose setæ of the mother's pleopods.

In this first stage the larvæ remained cowered down close to the pleopods and were so firmly fastened to the mother by their claws that they did not break loose when the pleopod was thrown into Worcester's liquid, though they jerked their legs and powerfully and violently flapped their abdomens. Those left locked to the pleopods of the mother lived three to four days and then molted into a second stage, May 26.

They were very large, 5 to 6 mm. long when stretched out and 4½ mm. as they lay with the weak abdomen carried forward under the thorax and were very attractive objects because of the swaying of the dark red and golden yolk mass, the contractions and change in color of the lobes of the liver spread like the fingers of a hand deep in over the back, and of the fiery, ruby-red, neuron-like, branching pigment cells spangled over a body so translucent as to show the white blood corpuscles hurried along the vessels over the red yolk, along the sinus at the edge of the carapace and out and in through the legs and antennæ like shuttles.

Camera lucida sketches of the first larva of *C. diogenes* showed it larger than even the second stage of *C. clarkii* but in simplicity and proportions essentially like the first stage. As usual in hatching crayfish the appendages were almost all bare of setæ; the eyes were nearly sessile; the rostrum a small triangle close to the body and between the eyes. The yolk far forward in the head-thorax distended that region and left the region for the gills and pereiopods of less extent.

In the first antennæ there were four segments in the larger, club-like exopodite and also in the slender, smaller endopodite and there were no sensory setæ.

The second antennæ were carried curved backward and downward but not close against the thorax as in *C. affinis* and each had only spines upon its scale and 35 segments on the slender part of the filament.

The mandible had no teeth but its edge was very slightly waved where the epidermal cells seemed about to secrete slight thickenings.

The scaphognathite used as a baling organ also was exceptional amongst the appendages in bearing plumose setæ which formed a row along the edge and were longer and more easily seen than in *C. clarkii.*

The gills were larger and with more side filaments than in *C. clarkii* but were suddenly reduced upon the fourth pereiopod so that the anterior arthrobranch had but a few filaments and the posterior none. On the last thoracic somite there were no gills, as is the case in all the young of Cambarus thus far studied.

The four pairs of pleopods had the endopodites slightly longer than the exopodites and the entire appendage was very much longer than in *C. clarkii* and with evident spines on both tips.

The telson with its enclosed pleopods was very much like that of *C. clarkii* and bore on its posterior edge the same kind of spines, about 14 on each side, six of which were specialized gland ducts arched over and joined together and bound to the telson string very much as in *C. clarkii,* figure 4. Inside the telson there were again the radiating glands making the plumose setæ of the second stage and a day before molting, the tips of the plumose setæ extended from their glands so far along, posteriorly, between the

epidermis and the loosened cuticle as to pass by several spines. Each new seta had its lateral barbs closely appressed against its axis. Moreover the new cuticle extended inward to line part of the seta gland so that in macerated specimens these cuticularized tubes ending abruptly, strongly recalled the like tubes that go in along the setæ of the earth worm. Probably at molting these sleeves become everted and so allow the sudden extension of the setæ to a length equal to the length of those tubes added to the length of setæ already lying between the old and new cuticles.

Molted into a second stage the young *C. diogenes* were 8½ mm. long, 1½ wide and 2 deep and had antennæ 5 mm. long. Until the next molt — some five days, May 26th to 31st,— they remained upon the mother's pleopods, but were not so firmly fixed as before as they fell off when put into Worcester's liquid.

While in most respects the larva was essentially like the second larva of *C. clarkii* a number of differences were noted.

The rostrum was less bent down than in *C. clarkii* and was long and pointed and visible from the side as its tip extended out beyond the eyes; its sides moreover were not straight as in *C. affinis* but arched so that something of the adult character was already expressed.

The first antenna was yet concave on the upper side of its base to fit against the eye and had in it a large open ear pit bordered externally by a few small spines and one very imperfect plumose seta. Beneath these spines the plumose setæ of the third stage were seen in formation. The exopodite bore seven sense setæ, three on the sixth and two on the fifth and on the fourth segments. The exopodites and endopodites were each divided into six segments.

The second antenna had some 13 to 15 plumose setæ on its scale and 38–42 segments on its filament.

The tips of the chelæ were still slightly recurved but as above noted the larvæ did not seem very firmly fastened by them.

Though the telson was larger than in *C. clarkii* its fringe of sparsely plumose setæ were noticeably shorter. There were about twenty on each side. In the base of the telson the large sixth pleopods showed a long exopodite, with a transverse joint, suggesting an index finger lying along the side of the telson while the endopodite was bent crosswise like a thumb.

A dissection of one of these second larvæ revealed a mass of membranous material and both simple and plumose setæ in the intestine suggesting that these larvæ may eat the egg cases and setæ from the mother's pleopods.

The creature was still translucent enough to show the ventral ganglia through the exoskeleton of the abdomen and was dotted over with pigment cells of stellate form, which when expanded were light red and when contracted very dark, while deeper in were diffuse and indefinite blue cells. In the antennæ and legs as well as in the antennal artery the corpuscles were going outward rapidly and returning somewhat more slowly in wider vessels.

Two days before molting into the third stage the new inner cuticle was already formed and the new setæ projected into the bases of the old. The yolk had become reduced to a small dark remnant on either side and even to the naked eye the gastroliths were conspicuous as two pink-white opaque areas, one on each side of the stomach enveloped in a clear glassy coat.

The third stage began by June 1st and had the adult character of a tail-fan made of the telson and the fully expanded sixth pleopods all fringed with perfect plumose setæ. These larvæ were $10\frac{1}{2}$ to 11 mm. long, 3 wide and $2\frac{1}{2}$ deep and expanded the tail-fan about 4 mm. while the antennæ were 6 mm. long.

These third stage larvæ when recently molted were still somewhat translucent and of a faint pink color with red-tipped claws and though the stomach was plainly visible the gastroliths were lacking on the outside. But within the actively moving stomach was a brownish liquid containing white particles or in some cases whole gastroliths moved about actively. In some cases the intestine contained colored material in its anterior part.

The specific gravity of the larvæ had so changed that they now floated in Worcester's liquid though the first and second stages sank; they were also less resistant to this fluid and died more quickly than when younger.

When the larvæ had changed into the third stage it was noted that the six mothers no longer had egg cases and cast cuticles upon their pleopods and as their fæces contained parts of plumose setæ of adult size it may be that they aided in cleaning off their pleopods though there is some evidence that the second larvæ may eat off

that material and Soubeiran stated that the young of an Astacus ate the egg cases and larval skins.

The third stage larvæ stayed near the mother some ten days or more, often, when disturbed, climbing on one another and crowding under and upon the mother, but after that they were quite independent and seemed to have no association with the mother though kept in the same small aquarium.

Walking and swimming the young sought food over the bottom of the aquarium and in a day cleaned off all the brown deposit from a spray of Myriophyllum and when another piece was given them ravenously set about tearing off and eating the bacterial slime and algal growths. When given Chara they seized an internode with their mouth parts and pushed it with their feet somewhat as a dog gnaws a bone, but when pieces of internode were cut off for them they seized them by one end and walked about sucking the contents out. Such a larva holding its head high and supporting a stick longer than its body, held by its mouth parts straight out in front of it, ludicrously suggested the enjoyment of a huge stick of candy. Animal food in the shape of a dead comrade was eagerly seized and pulled to pieces and a small earthworm was eaten up in a few hours.

Living thus, at a temperature of 85° F., the young were very active and darted away from the shadow of an object outside the water. After two weeks some molted without much change of size but by July 3rd some were 13 to 15 mm. long and the only survivor, July 15th, 18 or 19 mm. long.

From the above account it appears that the young of *Cambarus clarkii* and *Cambarus diogenes* associate with the parent in the first and second stages and in part of the third and this sort of family life is aided both by special recurved tips on the chelæ and by a peculiar telson thread; and as this is true also in *C. affinis* as well as in an Astacus of France and one in Oregon it is probably a general fact for all species of these two genera. Moreover all these crayfish show in the young structural characters and habits that make them unfit for free life like that of their marine relatives, the lobsters, and better fit them for a life of protected association with the mother with whom they live as in a kind of elementary family.

In this departure from ancestral conditions *C. affinis* has gone farther than Astacus in the following respects. In the first stage and in the second stage the telson is more reduced and both pairs of antennæ are more simple and to some extent this is also true in the other species of Cambarus here described. Thus in the first stage, Astacus has 50 to 66 spines along both the posterior and lateral edges of the telson while the three species of Cambarus have spines only upon the posterior edge and they are less than 30. Astacus also has in the first stage five segments in endopodite and exopodite of the first antenna and 50 in the filament of the second antenna while the three species of Cambarus have but four in the first case and 25 to 35 in the last.

In the first larval stage the three species of Cambarus thus agree amongst themselves and depart from Astacus in the direction of simplicity which is presumed to be a secondary reduction in connection with protected life upon the mother.

In the second larval stage *C. affinis* alone has spines merely and no plumose setæ upon its telson and is thus most remote from fitness for the active life of its ancestors. In the second stage Astacus is most like a free form in having its telson fringed with much more perfect and numerous plumose setæ than are found in *C. clarkii* or *C. diogenes*. In Astacus also the first antenna has its ear-pit well overarched by a row of plumose setæ but in *C. clarkii* there are only 3 or 4 plumes, in *C. diogenes* but one plume and in *C. affinis* only minute spines and no plumes. In Astacus the second antenna has 54 segments, in *C. diogenes* about 40, in *C. clarkii* 34 and in *C. affinis* 39. In *C. affinis* alone is there a retention of simple spines such as occur in the first larval stage, so that the scale of the second antenna here still bears no plumes.

Thus in the second stage *C. affinis* is most removed from Astacus but *C. diogenes* and *C. clarkii* depart less from the ancestral Astacus-like form.

Likewise in habit the three species of Cambarus agree in remaining attached to the parent during the second stage but in Astacus, however, as far as known, the larvæ become free in the second stage.

Apparently also Cambarus is more fitted to family life than is Astacus by having the anal thread at the time of passing from the first into the second stage.

From consideration of the larval life we come to the same general conclusion as that generally drawn from study of adult anatomy and geographical distribution, namely that Cambarus is a more highly evolved form than Astacus and that *C. affinis* is one of the higher, more specialized forms of the genus.

As to the relative position of *C. clarkii* and *C. diogenes* there is, however, doubt and discrepency. The adult characters seem to leave no doubt that *C. clarkii* is much the more primitive, less specialized and more like Astacus of the two. But in the adjustment of the larva to family life *C. diogenes* would seem to have progressed less far than *C. clarkii,* at least in the first stage *C. diogenes* has more segments in its second antenna and in the second stage more sense setæ in the first antenna as well as more segments in the second antenna. On the other hand *C. clarkii* would be more primitive in having more setæ over the ear-pit and if in nature the young actually get loose from the mother in the second stage they would be more like Astacus.

Yet in future study of crayfish it would seem that regard should be paid to the first three larval stages as aids in determining the relative positions of the species and their probable derivation from ancestral forms.

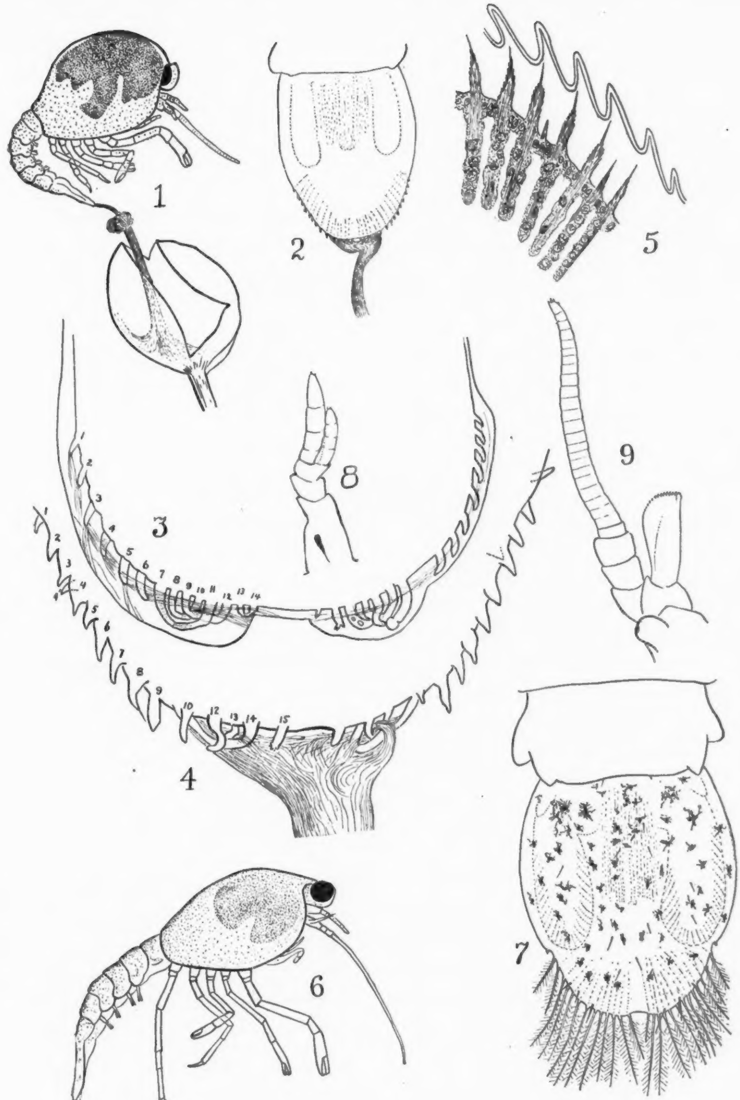
From a thorough study of larvæ of many species and from experiments in cross breeding some idea might be got as to the nature of the causes that seem to be leading some of the more evolved crayfishes to develop further that association of parent and offspring which forms in the crayfish a simple stage in family life.

December 20th, 1906

EXPLANATION OF PLATES.

All the figures were drawn with camera lucida and the Zeiss lenses indicated and were reduced to one third in diameter. They represent the first and second stages of *Cambarus clarkii.* Figures 1, 3, 6, 17 are from living and the rest from preserved specimens, fixed in Worcester's liquid.

FIG. 1. Larva just hatched from egg case with which it is connected by the telson-thread: 2.90 mm. a a.
FIG. 2. Dorsal face of telson of first larva with attachment of telson thread and internal pleopods, etc. 2. A.
FIG. 3. Dorsal face of end of telson teased out from egg about to hatch, showing investing cuticle over the glandular marginal spines. 2. D.
FIG. 4. Enlargement of part of such a view as Fig. 2, showing attachment of telson-thread to certain marginal spines. 2. D.
FIG. 5. Composite of surface views and sections of part of margin of telson of first stage. 6.4 mm.
FIG. 6. Right side of living larva in second stage. 2.90 mm. a a.
FIG. 7. Dorsal face of telson of second stage. 2. A.
FIG. 8. Dorsal face of left antennule of first stage. 2. A.
FIG. 9. Ventral face of left antenna of first stage. 2. A.
FIG. 10. Outer face of left mandible of first stage. 2. A.
FIG. 11. Outer face of left first maxilla of first stage. 2. A.
FIG. 12. Outer face of left second maxilla of first stage. 2. A.
FIG. 13. Outer face of left first maxilliped of first stage. 2. A.
FIG. 14. Outer face of left second maxilliped of first stage. 2. A.
FIG. 15. Outer face of left third maxilliped of first stage. 2. A.
FIG. 16. Posterior face of left chela of first stage. 2. A.
FIG. 17. Dorsal view of tip of chela of first stage alive. 2. D.
FIG. 18. Posterior face of left fourth pereiopod of first stage. 2. A.
FIG. 19. Anterior face of a left pleopod of first stage. 2. A.
FIG. 20. Tips of chela of second stage. 2. D.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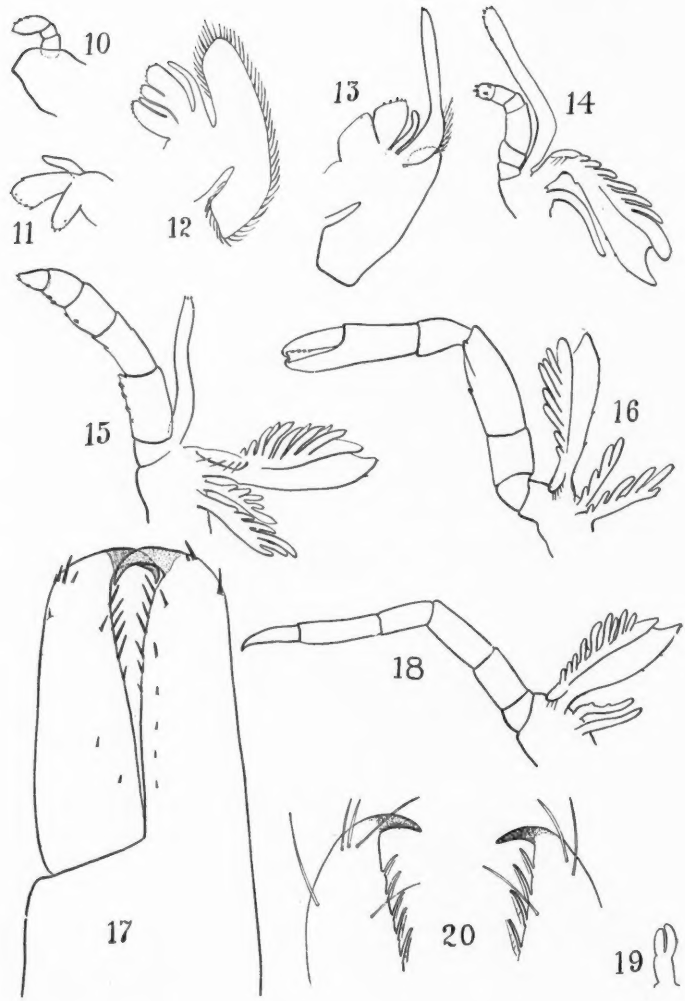
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NOTES AND LITERATURE

BIOLOGY

Beebe's Log of the Sun.[1] — Merely to turn over the pages of this beautiful book dispels all desire for captious criticism. The publishers have done everything to present it to the public in the best shape while the fifty-two full page plates in color by Walter King Stone and the numerous text figures from photographs and from wash and charcoal drawings make the work a delight unto the eye. Each of the fifty-two weeks of the year has its chapter; in some cases chosen with a full appreciation of the fitness of things, in others placed in position because one week would do as well as another. Some of these chapters have previously appeared, without illustration, in other places, while others were prepared expressly for this volume. Naturally the birds attract the most attention, with the mammals a close second, but other chapters deal with reptiles, fishes and insects, while the invertebrates of the sea are not neglected and even those marvels of crystallography, the snow flakes, have their allotted space. The text itself is written in an easy, graceful manner with a full appreciation of the wonders of nature and with the most sympathetic spirit. Here and there, perhaps, a statement is exaggerated or, may be, a slight mistake is made but these are but slight blemishes and they shall not be detailed here. Read the book, look upon the living world about you — sea, shore — plain or forest — with the open eyes of the author and you will see the marvels he has seen and a myriad others of which he tells you nothing.

Laloy's Parasitism and Mutualism. — Dr. Laloy devotes an introductory chapter of his recent work[2] to a consideration of the various reciprocal relations between living things of which series parasitism and mutualism are the opposite extremes. Following this the first part deals with parasitism under seven chapter headings: generalities,

[1] The Log of the Sun; a chronicle of Nature's Year. By C. William Beebe. New York, Henry Holt & Co., 1906, pp. xii + 345, $6.00.

[2] Parasitisme et Mutualisme dans la Nature, par le Dr. L. Laloy, bibliothécaire de l'Académie de Médecine. Préface de M. A. Giard, professeur à la Sorbonne. 1 vol. Bibliotheque Scientifique internationale; 82 text figures. 6 fr. Félix Alcan, éditeur, Paris 1906.

plant parasitism, plants parasitic on animals, animals parasitic on plants, animal parasitism, the rôle of parasites in pathology, and finally parasitism in the evolution of species. This last chapter presents in striking fashion an opinion previously advanced by this author regarding embryonic and sexual parasitism.

In the second part, devoted to mutualism, are grouped under separate chapters discussions of social life among plants, mutualism between plants and animals, social life among animals, and mimicry. Under these headings are discussed many interesting questions of an unusual sort. The author has selected instances of an illustrative type and presents them clearly and attractively.

The scope of the work is uncommonly large, embracing as it does both plants and animals and scant 300 pages are narrow limits in which to present such discussions in a form to escape criticism. To a zoologist it appears as if on the whole too great space had been given to the plant side and yet this may be distorted perspective on the part of the reviewer. The figures deal almost exclusively with plants and insects, with the former largely in the majority.

In many respects the work hardly represents present knowledge on the subjects discussed. Thus, in speaking of the hookworm, to which the author devotes a considerable section, the statements that this parasite sucks blood is perhaps excusable, though in 1903 Looss showed it to be incorrect, and this work has been much commented upon and quoted, as well as confirmed, since then. However to outline the life history with the larva encysted in a resistant envelope and infection taking place by the mouth is astonishing in view of the experimentation and discussion in this field for the past three years or more. Other statements are open to the criticism at least of serious exaggeration, such as that Yellow Fever caused one hundred deaths per annum in Havana under Spanish rule, or that in the Tæniæ one finds only internal autofecundation.

On the other hand the accounts of malarial organisms, of yellow fever and of trypanosomes are as good as could be given in the space at command. In the latter cases use was made of the admirable work of Blanchard, Laveran and Mesnil, while in the former the authority cited was not so trustworthy. In fact the author does not seem to know the literature of his subject thoroughly. He cites almost alone the French authors and does not differentiate clearly their work. Where his selection is happy the text is admirable, but at times the choice of an authority is less fortunate and the text suffers.

Some lack of knowledge shows itself also in the use of such long

since abandoned names as *Tænia cucumerina* and *Distomum hepaticum.* Better figures could have been found almost anywhere than those he gives of *Tænia solium* and tapeworm embryos; that of *Cœrurus cerebralis* is clearly wrong and the cut of a liver fluke is little more than a blotch of ink. On the other hand many of the botanical illustrations are excellent, and none are really poor. Neither authority nor credit is given for any figure, though many, if not most of them, are copied from other authors.

Despite these criticisms and an evident lack of control of his field in some places, Dr. Laloy has produced an usable work. The material brought together here is scattered widely and both unknown and inaccessible save to the specialist. The order is logical, the presentation clear and the author manifests the characteristic French ability to secure and hold the attention and interest of his readers.

GEOLOGY

Relative Geological Importance of Continental, Littoral, and Marine Sedimentation. — Professor Joseph Barrell has given us[1] a critical discussion of the conditions under which continental, littoral, and marine sedimentation take place, the classification of the three types of deposits, the evidence upon which they may be discriminated, and the probable areal and vertical extent of the deposits of each class now found in the geological column. It is shown that the littoral zone is of exceedingly small extent, its deposits less likely to be preserved than the deposits of the other two zones, and that unless a given formation is undoubtedly of littoral origin it is more likely to be either marine or continental. The regions of continental sedimentation are shown to be far more extensive than generally believed, the chances for the preservation of continental deposits often very good, and that therefore a much greater proportion of ancient sediments is likely to be found of continental origin than is generally conceded. The last part of the essay deals with the origin and preservation of mud cracks, and their value as a criterion of continental rather than of littoral sedimentation. It is shown that contrary to the usual interpretation, mud cracks generally furnish one of the surest

[1] Journal of Geology, **14**, pp. 316–356, 430–457, 524–568, 1906.

indications of the continental origin of a given formation. Applying the results of his studies to specific portions of the geological column, the author concludes that certain important formations, heretofore generally referred to a marine origin, are most probably continental deposits.

Professor Barrell's paper is an important contribution to a series of studies which are resulting in a very manifest movement away from the former tendency to regard all sediments as marine unless definitely proved of some other origin, toward a fuller recognition of the importance of continental sedimentation, and a more open attitude of mind to such an alternative interpretation.

D. W. J.

Observations in South Africa.— Professor W. M. Davis presents[1] a variety of geological and geographical observations made during his visit to the Colonies of South Africa in the summer of 1905. After a brief introduction, in which the going and return journeys are sketched, the physiographic provinces of South Africa are outlined, and the problems to be considered briefly stated. The next twenty pages are mainly concerned with a study of the Cape Colony ranges considered with special regard to their resemblance to the Allegheny mountains of our own country, both groups belonging to the class of much dissected folded mountains. The famous Dwyka glacial formation of Permian age is next discussed in some detail, some twenty pages dealing with the character of the evidence upon which reference to a glacial origin is based, the topography of South Africa during Dwyka time, and the possible causes of the Dwyka glacial period. The third portion of the paper deals with the peneplain of the Veld or interior highland, and the conditions of its origin, the evidence being weighed with a desire to discriminate if possible between normal peneplanation as one alternative, and arid leveling without baseleveling as the other. Other problems of interest, such as the origin of the zig-zag gorge below the Victoria falls of the Zambesi, and the probable greater extent of South Africa in former times, are considered. Eight plates and a number of drawings serve to illustrate the paper.

D. W. J.

Geology of the Big Horn Mountains.[2]— The results of five seasons' field work in the Big Horn Mountains of Wyoming and Montana

[1] Bulletin Geol. Society of America, **17**, pp. 377–450, 1906.

[2] U. S. Geological Survey, Professional Paper No. 51, 1906, 128 pp.

are embodied in this splendidly illustrated report by Mr. N. H. Darton. After a preliminary consideration of the geography of the region, an extended and detailed account of the various types of rocks represented in the range is given. The glacial geology is discussed by Professor R. D. Salisbury on the basis of work done by several assistants. The results of glacial erosion are very pronounced, splendid examples of cirques, U-shaped valleys, and glacial lakes being found, the amount of valley-deepening due to glacial scour being placed as high as 700 feet or possibly more in cases. The structure of the range is next considered, the uplift being in the nature of a great anticline with a somewhat prominent local dome toward the southern end, while minor flexures and faults occur. The general geologic history of the region is traced, and in conclusion the mineral resources, water supply and timber are described. Some years ago Mr. F. E. Matthes prepared an unusually valuable contour map of the central portion of the range and discussed the feature due to glacial sculpture Mr. Darton's report gives a comprehensive account of the general geology, adding much to our knowledge of this interesting region.

D. W. J.

A Glacial Lake in Tibet.— Mr. Huntington has spent several seasons in the study of geological and geographical features in central Asia, and presents in this paper[1] an account of a lake which seems to owe its origin to glacial erosion, and which closely resembles the famous valley lakes of Switzerland. According to previous observers the lake has been formed by the damming of an old outlet by fans spread out across the valley by tributary streams; but Mr. Huntington presents pretty clear evidence that the basin is terminated by a rock lip rising well above the present level of the lake, and of course much farther above the lake bottom, the lake being 142 feet deep according to F. Drew. There seems to be no evidence of warping or faulting, while the evidence of strong glaciation is abundant. The features observed would seem to indicate a true rock basin of appreciable depth scoured out by the valley glacier. Fluctuations of climate are recorded by a number of elevated beaches marking oscillations of lake level. The paper is illustrated with a map and numerous drawings and photographs.

D. W. J.

[1] Pangong: A Glacial Lake in the Tibetan Plateau. By Ellsworth Huntington. Journal of Geology, Vol. 14, 599-617, 1906.

ZOÖLOGY

A Statue of Lamarck.— As yet there is no memorial to this eminent naturalist but now it is proposed to erect one in the Jardin des Plantes in Paris. The matter is in charge of a committee of the Museum d'Historie Naturelle in Paris; subscriptions may be sent to Professor Joubin, the secretary, 55, Rue de Buffon, Paris, France.

Gardiner's Maldive and Laccadive Archipelagoes,[1] parts of which have been noticed in these pages as they have appeared, has now been completed. The whole makes two quarto volumes of 1079 pages and 100 plates. In this concluding part is an account of the Myriapoda collected by R. I. Pocock enumerating eight species, and some supplementary remarks upon geographical distribution and comments upon the coral reefs, apropos of Mr. Agassiz's work in the same region.

Kollmann's Atlas of Human Embryology.[2] — This is, as its name implies, an atlas of development. There is no true text, merely descriptions of the three hundred and forty figures which are intended to illustrate the features of human embryology. These figures, which are in part printed in tint, in part in color, are of varying degrees of artistic excellence and have been taken from various sources, a goodly proportion of them being original. Those in half-tone made from wash drawings are with few exceptions excellent, while those made by the zinc process are usually more crude. In a few cases other animals than man have been called upon to supply the illustrations. Thus the early phases of the mammalian orums are based upon Sobotta's well known figures of the egg of the white mouse; Bonnet's work upon the dog and Selenka's upon the apes are called in to illustrate other early features; while chick and fish furnish illus-

[1] The Fauna and Geography of the Maldive and Laccadive Archipelagoes edited by J. Stanley Gardiner, Volume 2, Supplement 2, Cambridge [England] 1906. 3s, 6d.

[2] Handatlas der Entwicklungsgeschichte des Menschen von Dr. Julius Kollmann, Erster theil; Progenie, Blastogenie, Adnexa Embryorum, Embryologia Osseum, Embryologia musculorum. Jena, Gustav Fischer, 1907. Mk. 15, Gebunden.

trations of monstrosities, and the development of the skull is introduced by Schauinsland's figures of Callorhynchus, and Stöhr's of the salmon.

While the work has considerable value for the medical student in that the illustrations supplement those of the usual text book, the morphologist finds the volume less adapted to his needs. One might wish figures showing the early stages of the vertebral column, more details regarding the development of the lower jaw, better illustrations of the embryonic adnexa, and some connection between the figures of the head cavities and the definitive eye muscles which develop from them. Three figures illustrate the development of the diaphragm. In two only the septum transversum is shown; in the third the diaphragm has nearly its definitive condition, but there is nothing to show the origin of the 'pleural portion.'

The Systematic Position of the Tubinares.— In a recent number of this journal (**41**, p. 111, 1907), Dr. Shufeldt in the historical introduction to his paper 'On the osteology of the Tubinares,' has this to say about my treatment of these birds in the Standard Natural History, vol. IV, pp. 84, seq., (Boston, 1885): "This writer places in his scheme the Tubinares widely removed from the Steganopodes, which I believe to be a mistake, and a non-appreciation of the morphological characters of the latter group of Birds."

If the main object of the bird volume of the Standard Natural History had been to present a new classification which in all details should represent my own ideas, the position of the Tubinares would have been a different one. That I fully indicated their proper place and also fully appreciated their 'morphological characters' will be apparent from a perusal of the following quotations from my work: "The arrangement may not be regarded as final, however, for there are reasons to suspect that it will be necessary, ere long, to divide the schizognathous swimmers into three orders, Eretmopodes for the first two superfamilies of the present arrangement, Tubinares for the superfamily Procellaroideæ, and Pluviales for the rest." (P. 65.)

"It has already been hinted at, on a previous page, that the superfamily Procellaroideæ might perhaps better constitute a separate order, Tubinares. Their differences from all the foregoing birds are many and important, and their affinities seem to be more with the Steganopodes and Herodiones than with the gulls or the auks, to some of which many of the petrels show a remarkable external and superficial resemblance." (P. 84.)

And finally, on page 85, I again emphasized the true position of these birds by reiterating that it is "rather probable that the Tubinares should be placed in the neighborhood of the Steganopodes and Herodii."

Professor Fürbringer, in his last review of this subject (Jena. Zeitschr. Naturw., **36**, pp. 644–646, 1902), does full justice to the subject as follows: "Stejneger–Cope ('85/'89) follow Huxley in the rather unfortunate establishment of the Cecomorphæ, but Stejneger mentions particularly that the Tubinares perhaps are better regarded as a special ordo with nearer relation to the Steganopodes and Herodii.... On the strength of later considerations I still adhere essentially to the opinion expressed by me in 1888, but I am inclined to place their relationship to the Ciconiiformes more in the foreground and that to the Laro-Limicolæ more in the background than then.... On the other hand, I cannot follow those authors who argue for placing them too far from the Laro-Limicolæ," the group called *Pluviales* by me in my first quotation above from the Standard Natural History.

LEONHARD STEJNEGER.

Beebe's The Bird[1] in the American Nature Series is easily one of the most useful as well as one of the most interesting books which this epoch of bird books has produced. It marks, we hope, the beginning of a new period in amateur bird study, a period when many of those who now keep bird lists as a pastime will take up the serious study of the bird itself. The book contains seventeen chapters, the titles of some of which are as follows,— The Framework of the Bird, The Skull, The Food of Birds, The Senses, Beaks and Bills, The Eggs of Birds, etc.

Mr. Beebe is curator of birds in the New York Zoological Park. His position has enabled him to observe at close range the habits of a great variety of birds, and also to discover the needs of an inquiring public. Mr. Beebe is, however, much more than a keeper of animals; he is a trained scientist and a skilful lecturer. He has succeeded in this book in arranging a large amount of accurate information clearly and forcibly, and to present it in such a way as to arouse and hold the reader's interest.

The value of enlarging the amateur student's horizon is constantly

[1] Beebe, C. William. The Bird. Its Form and Function. New York, Henry Holt & Co. x + 496 pp. 371 figures.

in the author's mind. The first chapter, therefore, presents the essential facts which palæontology contributes to our knowledge of the bird, and throughout the book there are frequent and illuminating references to homologies or analogies in the kindred classes. The delicate balance of Nature and the complex interrelations of all organic life are well illustrated in the chapter on food.

Where a large number of forms are discussed it is difficult to avoid the appearance of a mere catalogue of compiled facts. Evans' Dictionary of Birds is a noticeable example of work of this kind. Mr. Beebe has avoided this danger by a happy introduction from time to time of bits of personal observation, or by enlarging on some exceptionally interesting habit or structure. The reference to a flamingo observed by Mr. Beebe, weeping from terror because a condor was playfully "galloping" around it, illustrates also the author's happy choice of words.

The suggestion of problems to the solution of which careful observers can bring assistance, the frequent references to Nature's evasions of our pet theories, and the conservative position taken on disputed points, begets in the reader a strong and deserved feeling of confidence that Mr. Beebe possesses together with his power of picturesque presentation the wide knowledge and sound judgment of a trained scientist. Mr. Beebe is evidently a strong believer in sexual selection, but he puts forth (p. 318) an interesting suggestion that the display of the male bird instead of affecting the æsthetic sense of the female may induce some sort of hypnotic condition. In the chapter on The Body of the Bird (pp. 292–295) there are some interesting observations on color changes due directly to environment or food. White-throated sparrows and wood thrushes turned almost black when confined in a bird house where the air was constantly moist.

The book is extremely rich in illustrations, chiefly photographs of great clearness and beauty taken from life by the author. Their excellence adds much to the attractiveness of the work, and the skill with which they have been selected and arranged is evidence of the author's gift as a teacher. There is an excellent index, and a brief list of useful books.

Though primarily intended for the instruction of amateurs, Mr. Beebe's book is one that will at once win an honorable place in the library of every teacher of natural history. No public library or school should be without it. It will be the hope of all who use this manual, that Mr. Beebe will follow it by a similar treatment of the intelligence of birds.

R. H.

The Conus Arteriosus in Teleosts.— One of the characters which have been relied upon to distinguish Ganoids from Teleosts has been the presence in all Ganoids and, with the exception of Butirinus, its absence from all of the other group. H. D. Senior now shows[1] that the tarpon of our southern waters has a conus with two rows of valves.

Does half of an Ascidian Egg give rise to a whole Larva?— In reply to criticisms of Driesch, Conklin returns to this question which was discussed in his earlier papers and maintains (Archiv f. Entwicklungsmechanik, **21**, 1906) the general correctness of his former account. The half blastomere cleaves as if it were still part of the entire egg; correspondingly the resulting gastrulæ are half gastrulæ and are in no wise bilaterally symmetrical and the anlagen of muscles and mesenchyman unilateral in position. Similarly the larvæ up to the time of metamorphosis are half larvæ, having only the parts belonging to one side—right or left—represented. They "are such as would result if a fully formed larva were cut in the median plane and the cut edges of each half then came together, the dorsal and ventral mid-lines joining. These results follow from the early differentiation of the organ-forming substances in the egg.

Digestive processes in Collembola.— Dr. J. W. Folsom and Miss M. U. Welles have studied the digestive processes in the mid-gut of Tomocerus and other Collembola.[2] They deny the existence of Malpighian tubules in these insects and note the fact that they molt throughout life. In connection with each ecdysis there is a degeneration of the inner half of the intestinal epithelium, the degenerate portion being cast out soon after the molt, carrying with it a part of the nuclei which are replaced mitotically from those which persist. In this degenerating mass is contained sodic urate as well as gregarine so that this is an excretory process. Adult specimens molt every six or eight days; the cast skin is devoured.

Fresh Water Amphipods of North America. — Miss Ada Weckel furnishes a valuable synopsis[3] of these forms. In all eighteen species are described, two (*Gammarus ramellus* from California and *G. cæcus* from Cuba) being new. The author seems to have overlooked

[1] Biological Bulletin, **12**, 1907.
[2] University [of Illinois] Studies, **2**, no. 2, 1906.
[3] Proc. U. S. Nat. Mus., 32, 1907.

the description of *Crangonyx knoxensis* by O. P. Hay printed (June 27, 1878) on the extras of Dr. Hay's reprint of his "Description of a new species of Asellus" from the Bulletin of the Illinois State Laboratory of Natural History, No. 2. This reprint, by the way, possesses a plate, illustrating *Asellus militaris, Crangonyx knoxensis* and *C. gracilis* Smith, which does not appear in the Bulletin.

Some Problematic Worms.— Schepotieff has a valuable systematic paper[1] on the interesting worms of uncertain affinities grouped as Desmoscolicidæ, Echinoderidæ, Chætosomatidæ, and Rhabdogaster and Trichoderma. The article begins with some interesting conclusions as to geographic and bathymetric distribution and then proceeds to the description of the species, illustrated by good figures, in which numerous new forms are recognized.

C. Davidoff thinks[2] that he has found evidences of a true mesoderm in the larva of the Narcomedusan jelly fish Solmundella. Photographs of sections which he gives show a distinct cell-layer between ectoderm and entoderm, not the structureless mesoglœa usual in that position. If this interpretation be correct, it will, as Davidoff remarks, remove one of the objections to a close association of Ctenophores with the Cnidaria.

Leisenitz has studied[3] the chitinose spines occurring on a number of insect larvæ which serve as organs of locomotion. Numerous zinc etchings illustrate the kinds of spines and their arrangement. The results are not readily summarized and have little systematic importance.

Forbes' Keys to Lepidoptera and Caterpillars[4] will doubtless prove of value to beginners in the study of the butterflies of New England, while others will find the keys to the larvæ of use. First in order is a list of butterflies and larger moths with size and color markings, food plants of the larvæ, dates of imago, number of broods and haunts; next a key based upon color of the species of large Lepi-

[1] Zoologischer Anzieger, **31**, p. 132, 1907.

[2] Zoologischer Anzeiger, **31**, p. 119, 1907.

[3] Ueber chitinöse Fortbewegungs—Apparate einiger Insektenlarven. München, 1906.

[4] Field Tables of Lepidoptera by Ww. T. M. Forbes, Worcester, Mass., 1906, pp. 141.

doptera found in New England. The second portion (over half) is given to a key to the caterpillars of all but the smaller Lepidoptera of the same region.

J. F. McClendon has described four new species of Myzostoma (Proc. U. S. Nat. Mus., 32, 1907, obtained from the collection of crinoids in the National Museum.

BOTANY

Sukkulente Euphorbien.[1]—This is the first of a series of illustrated handbooks of succulent plants designed by the author to meet the demand that the scattered literature should be brought together in a form accessible to the many cultivators of this group of plants. The aim is to give both a scientific classification and cultural hints on those species now in cultivation and this work has been admirably done, both in the text and in the numerous half-tone illustrations.

One hundred and nine species and eight varieties of Euphorbias are treated, nine species and two varieties being new to science and three species have been renamed. The species listed are for the most part natives of Africa, though a few are from the adjacent islands and from India, and three are American. A good working key is given to the twelve sections under which the species are arranged and the sections again are each provided with good comprehensive keys so that a species may be readily determined. The descriptions are full and clear, supplemented by full synonymy and by additional notes on habitats and comparisons between species, ending in a short note on the culture required for the species. Following the treatment of species a chapter is devoted to the general culture required for this group of succulents and the text ends in a full index to the literature bearing on the group.

In view of the fact that several new species appear in the publication it may be well to state that, though the title page bears the date of 1907, copies have been distributed in December 1906.

C. H. Thompson.

[1] Berger, Alwin. *Sukkulente Euphorbien.* Stuttgart, 1907. 12 mo. v + 135 pp. 33 Abb.

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